Koala and Possum Populations in Queensland during the Harvest Period, 1906-1936

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ABSTRACT

The Queensland Koala *Phascolarctos cinereus* and possum harvests were regulated from 1906-1927 and 1906-1936, respectively. Before that, there was an uncontrolled harvest. Historical data from the harvest period were analysed to gain information on *P. cinereus* and possum (mainly *Trichosurus vulpecula*) population ecology and status. *P. cinereus* numbers peaked in southern Queensland around the turn of the century or in the first decade of the 20th century. In central Queensland, they peaked later, probably in the 1920s, and in north Queensland there does not appear to have been any pronounced fluctuation in numbers. *P. cinereus* populations experienced diseases similar to those occurring today. Chlamydial diseases were common and occurred in most parts of the State, with cystitis being more common. Some diseases were not clearly identified. In contrast to current populations, *P. cinereus* populations then had many more episodes of high mortality, population size appears markedly more volatile and overall abundance was much higher. Southern Queensland populations declined greatly at the time of the harvests, but the central Queensland population expanded after the last harvest and harvest mortality does not provide an adequate explanation of population decline. Although it is sometimes said, particularly with regard to island populations, that Queensland (and New South Wales) *P. cinereus* populations differ from those of Victoria in that they do not exhibit local irruptions and excessively high abundance, the population phenomena appear similar to those occurring in Victorian populations. Queensland populations achieved very high growth rates that resulted in unsustainable population densities and, eventually, mass mortality. Possum populations were subject to very high harvests that were apparently sustainable, at least in the short term, and showed fluctuations that were partly similar to those of *P. cinereus*.

The *P. cinereus*, and probably also the possum population fluctuations, are mostly consistent with models of herbivore irruptions. The koala population fluctuations are interpreted in terms of herbivore irruption theory. We suggest that koala population expansion was a response to an increase in food availability (possibly due to the development of regrowth vegetation and/or waves of dieback) resulting from land development patterns. A subsequent decline in food availability, accompanied by severe outbreaks of chlamydial disease (probably due to poor nutrition), led to severe declines in koala population size, often to levels well below the apparent carrying capacity. Populations of at least some possum species (*T. vulpecula* and possibly *P. peregrinus*) also appear to have experienced irruptions and declines, but the fluctuations do not correlate as closely with major aspects of the development of land for pastoralism and agriculture as do the changes in *P. cinereus* populations. Specific factors responsible for the expansion and decline of *T. vulpecula* and *P. peregrinus* populations were not identified. Very high harvests in 1919 and 1920 also seemed to affect possum numbers.

Key words: Koala, possum, fur trade, wildlife harvest, *Phascolarctos cinereus*, *Trichosurus vulpecula*, koala abundance, koala disease, population irruption

Introduction

The distribution of the koala *Phascolarctos cinereus* in Queensland has contracted greatly since European settlement due to clearing of forest and woodland, resulting in severe local contractions. It is likely that population size also contracted greatly. This decline in status is often attributed to over-harvesting during the harvest period that ended in 1927. *P. cinereus* is currently undergoing further declines in many areas throughout the State due to clearing of forest and woodland. Habitat conservation is required to arrest these declines. Habitat protection is very poor and there is a high potential for a substantial decline over the medium to long term, particularly in inland areas if extensive clearing of habitat is not halted (ANZECC 1998). A Koala Conservation Plan currently being prepared by the Queensland Government may provide a remedy for this problem.

P. cinereus populations have experienced large fluctuations in population size since European settlement, including in particular a large increase in the late 19th century, usually attributed to the decline of Aboriginal hunting, and a subsequent decrease by the early 20th century (Parris 1948; Troughton 1967; Warneke 1978; Lunney and Leary 1988; Martin and Handasyde 1999). Details of the timing and size of population fluctuations are poorly known.

Similar population irruptions in macropods at about the same time have been described as herbivore irruptions in response to habitat change (Caughley 1977; Jarman and Johnson 1977). Jarman and Johnson described herbivore irruptions among macropods in New South Wales during the periods 1880-1887 for kangaroos, 1887-1913 for wallabies and 1907-1909 for "padamelons".

Common Brushtail Possums *Trichosurus vulpecula* experienced a similar population irruption in the New England district (Jarman and Johnson 1977) and possibly elsewhere. Kerle (2001) provides an account of an irruption and decline near St George, Queensland, during the 1880s and early 1890s. However, it is not clear how extensive this phenomenon was in possum populations.

The *P. cinereus* harvests and possum harvests were an opportunistic response to the population expansion (Strahan and Martin 1982; Hrdina and Gordon 2004). A new resource had become available and it was rapidly exploited.

The *P. cinereus* decline in the late 19th and early 20th century has been attributed to various causes, including harvesting for furs, disease, and clearing of habitat. Some observers at the time, such as Le Souef and Burrell, attributed the decline to disease, rather than the skin harvests. A disease described as "ophthalmia and periostitis of the skull" killed "millions" of *P. cinereus* from 1887-1889 and 1900-1903 (Le Souef and Burrell 1926). Because there was a great increase in numbers in the second half of the 19th century, the 20th century decline may also be viewed as a correction of the earlier increase in population size. A correction might occur if the increase had resulted in population sizes that were unsustainable over a long term.

In the late 19th and early 20th centuries, demographic processes occurred in *P. cinereus* populations that are now absent or rare in Queensland:

- The large population expansion from about mid-19th century referred to above.
- Mortality due to harvesting for the fur industry, commonly said to have caused a severe decline in *P. cinereus* populations in the late 19th and early 20th century.
- Naturally occurring local declines, or mass mortality, often accompanied by and attributed to conspicuous "disease" episodes, a phenomenon that occurs rarely now (e.g. Gordon *et al.* 1988).

In order to conserve *P. cinereus* today, it is important that we attempt to understand the processes affecting *P. cinereus* then, and identify any implications for population ecology now. The phenomena mentioned above presumably had a major effect on population size and trends at the time. In this paper, we analyse historical records associated with the *P. cinereus* and possum harvests in Queensland and present information on population trends and disease. We also attempt to identify the impact of the fur harvest and other factors on *P. cinereus* populations in Queensland.

Table 1. Examples of questions circulated to government officers asking for opinions on the status of koalas and possums. The table shows the questions used in letters from the Department of Agriculture and Stock to government officials each year. Sources: Queensland State Archives: Department of Agriculture and Stock. (1) AGS/J201 file 2003. 1923. Summary of reports on open season, 26/3/1923. (2) AGS/J325 file 545B. 1925. Memo from Constable McCreath, Stonehenge, 13/1/1925. (3) AGS/J565 file 604. 1929. Memo from Under Secretary Department of Agriculture and Stock, 3/4/1929.

January 1923
(a) Whether opossums are sufficiently plentiful in your district to warrant opening the season for trapping say from the 1st May?
(b) Were there many trappers following that occupation during the season of 1922 in your district?
(c) Are the native bears sufficiently numerous in your district to warrant the consideration by the Minister of a trapping season in 1923?
(d) Has a disease been noticed among native bears? If so, the extent and to what it is attributed.
January 1925
(a) Whether opossums are sufficiently plentiful in the district, to warrant opening a season for trapping?
(b) Are the native bears sufficiently numerous in the district to warrant the consideration by the Minister of a trapping season in 1925?
(c) Has a disease been noticed among native bears, if so the extent and to what it is attributed?
January 1929
(a) Opossums are plentiful
(b) Native bears are plentiful
(c) Opossums are fairly plentiful
(d) Native bears are fairly plentiful
(e) Opossums are scarce
(f) Native bears are scarce
(g) No opossums
(h) No native bears
It is also desired that you will specify the localities in your district, if any, where the opossum and native bear are to be found.

Methods

Hrdina and Gordon (2004) describe the sources of information. Material from the Queensland State Archives is cited with the bundle number and file number, e.g. "AGS/J201 file 2003".

P. cinereus and possums were harvested in Queensland from 1906-1927 and 1906-1936 respectively. Harvests were regulated by the Fauna Acts (Hrdina and Gordon 2004). Before 1906, unregulated harvests occurred. Possums mainly comprised the Common Brushtail Possum *Trichosurus vulpecula*, but also included a number of other species in some areas, including in particular the Mountain Brushtail Possum *T. caninus* and the Common Ringtail Possum *Pseudocheirus peregrinus* (Hrdina and Gordon 2004).

From at least 1922, government officials throughout the State were asked to report on the status of koalas and possums, i.e. whether they were sufficiently plentiful to sustain a trapping season. The estimates of status are based on their opinions, and on information obtained from local people. Most reports came from stock inspectors, land rangers and police, but also from a few other officials including pear (i.e. the cactus *Opuntia* spp.) rangers, forestry rangers and foresters. In 1926, reports were provided by Opossum Board members, and from 1927, by Rangers appointed under *The Animals and Birds Acts, 1921 to 1924* (Hrdina and Gordon 2004). A few miscellaneous reports are also available for this period. The Department of Agriculture and Stock collated this information, usually in January or February, and used it to assist in making a decision on opening the season in the following autumn/winter (Hrdina and Gordon 2004). Table 1 shows examples of the questions for some years. Some opinions on populations were also found in other departmental correspondence, particularly with regard to koalas. This correspondence usually came from people or groups either objecting to open seasons or advocating open seasons.

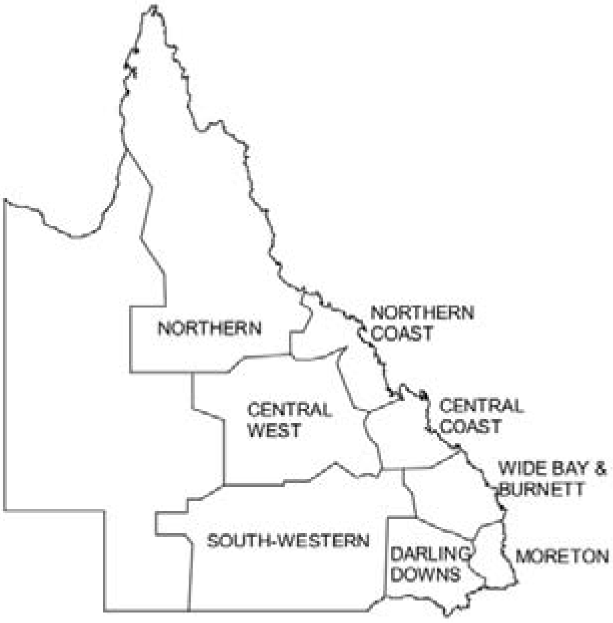

Figure 1. Queensland, Australia. Map of Opossum Districts. Boundaries are approximate.

The reports describe numbers at the time of reporting (i.e. usually January or February) or over the preceding few months. Information obtained in 1923, 1924 and 1925 yielded about 200-300 responses each year. The best data are available from 1922-1936. Opinions of government officials were sought for at least some years before 1922, but the correspondence was not retained in departmental files, and information is scarce for that period.

In the analysing the data for this paper, the opinions of population size were grouped by the eight Opossum Districts (Hrdina and Gordon 2004) (Figure 1) and classified into a status category: Scarce, Uncommon, Common or Abundant. Examples of the reports given by correspondents are shown in Table 2, with our interpretation of such opinions as status categories. The four categories were given numeric scores from 1 to 4, and a mean score for status per Opossum District per year was then calculated for *P. cinereus* and possums.

Sample sizes were low, usually one or two reports per District before 1923 (Appendix 1), and status categories were treated with caution for this period. Although many sample sizes were also low from 1927 on, these data are more reliable because they mainly originate from Opossum Boards and Fauna Rangers. Reports of mortality and disease were obtained from the same sources as indicated above. In some years (e.g. 1923, 1925, Table 1), officials were specifically asked to report any koala disease that was present. Places mentioned in the text are shown in Figure 2.

Interpretation of numbers from reports

Some correspondents gave numerical examples of population status. Assessing Land Commissioner H.A. Watson wrote of south-western Queensland in 1923: "During the past three years, and travelling over hundreds of miles of country, I have not seen more than a hundred bears. They are practically wiped out"[1]. This rating is classified as "Scarce" here, based on the statement "They are practically wiped out". Observers in the early 20th century were aware of the very high abundance around the turn of the century, which they apparently thought of as "normal", and appeared to calibrate their ratings against that level: thus if numbers seen were substantially lower, it was taken as evidence of near extinction. However, a modern observer of koalas would probably rate such an observation at least one level higher, i.e. as "Uncommon", or possibly even "Common", based on the number sighted. If a casual, non-expert observer saw 100 koalas in western Queensland today, it would be taken as evidence of relatively good status. It would certainly not be seen as evidence of near extinction. In this analysis, interpretation of numbers from observer's comments (Table 2) is based directly on the observer's opinions, unless there is convincing evidence otherwise.

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[1] Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Summary of reports on open season, 26/3/1923.

Table 2. Examples of statements of status of koalas and possums found in departmental files and elsewhere, and their interpretation as one of four status categories: Scarce, Uncommon, Common, Abundant. "Rank" shows the numerical rank assigned to each category.

Opinion	Interpretation	Rank
Almost extinct	Scarce	1
Almost unknown	Scarce	1
Extinct	Scarce	1
Nearly extinct	Scarce	1
Practically extinct	Scarce	1
Practically annihilated	Scarce	1
Odd bears	Scarce	1
Only a few, on streams	Scarce	1
A few	Scarce	1
Very few	Scarce	1
Very rare	Scarce	1
Very scarce	Scarce	1
Fast disappearing	Scarce	1
Few	Scarce	1
None seen in last 6 months	Scarce	1
Rare	Scarce	1
Scarce	Scarce	1
Insufficient [for an open season]	Uncommon	2
Just appearing in district	Uncommon	2
Not common	Uncommon	2
Not numerous	Uncommon	2
Not plentiful	Uncommon	2
Not sufficiently plentiful [for an open season]	Uncommon	2
Not very plentiful	Uncommon	2
Uncommon	Uncommon	2
Common	Common	3
Becoming numerous	Common	3
Fair	Common	3
Fair number	Common	3
Fairly Numerous	Common	3
More numerous than for many years past	Common	3
Numerous on forest reserves	Common	3
Plentiful away from settlement	Common	3
Plentiful in some parts	Common	3
Reasonably plentiful	Common	3
Recovered	Common	3
Sufficient [for an open season]	Common	3
Sufficiently plentiful [for an open season]	Common	3
Any amount of bears	Abundant	4
Considerable amount of bear in district	Abundant	4

In great abundance	Abundant	4
Large numbers all over	Abundant	4
Numerous	Abundant	4
Plentiful	Abundant	4
Plenty of possums	Abundant	4
Thousands in rough country	Abundant	4
Very numerous	Abundant	4
Very plentiful	Abundant	4
Very thick	Abundant	4

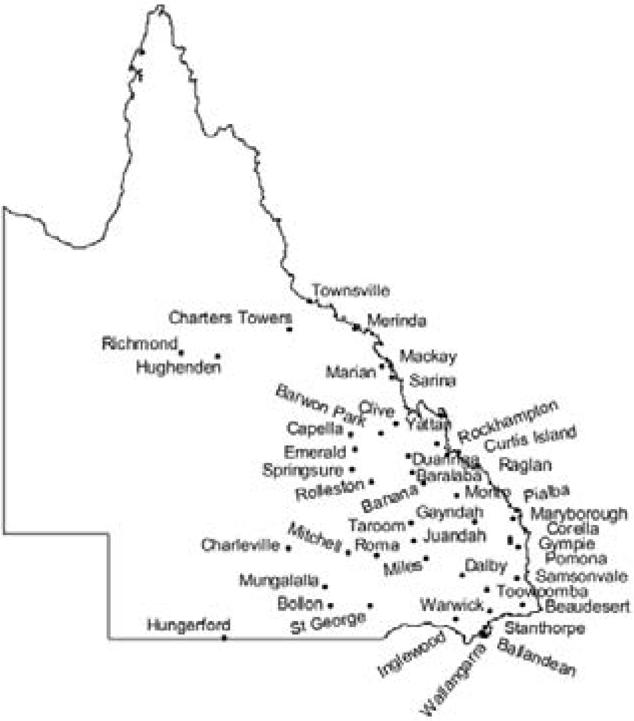
Townsville
Charters Towers
Merinda
Richmond
Hughenden
Mackay
Marian
Sarina
Barwon Park
Clive
Yatta
Rockhampton
Capella
Curtis Island
Emerald
Duaringa
Raglan
Springsure
Baralaba
Rolleston
Banana
Monto
Pialba
Gayndah
Maryborough
Taroom
Corella
Mitchell
Juandah
Gympie
Charleville
Roma
Pomona
Miles
Dalby
Samsonvale
Mungalalla
Toowoomba
Bollon
Warwick
Beaudesert
Hungerford
St George
Stanthorpe
Inglewood
Ballandean
Wallangarra

Figure 2. Queensland, Australia. Places mentioned in the text.

In 1907, John Davies of Pomona wrote that bears "are getting very scarce and will soon be extinct"[2]. He went on to complain that a week earlier some men had gone onto his land where the bears "were a bit plentiful" and shot 18 bears in one night. Most observers now would regard a take of 18 bears in a night as an indication of common or abundant status, whereas Mr Davies thought bears were very scarce, although admitting they were a "bit plentiful" on his property. This observation was interpreted as evidence of common status in the analysis as he stated that they were a "bit plentiful" on his property.

P. cinereus and possums are relatively inconspicuous to lay observers and their estimates of numbers should be treated with caution, and usually as under-estimates. It has been a common experience for one of the authors (G.G.) to be told by farmers that *P. cinereus* were absent from their properties when subsequent searches showed them to be relatively common. Most of the reports during the harvest period came from public servants, including stock inspectors, police and land rangers, who had no training in wildlife management and probably little aptitude for natural history. There was often strong divergence of opinion on the status of koalas and possums among observers at the time. Government officials were apprehensive about the impact of the fur harvest on koala populations (Hrdina and Gordon 2004), and possibly did not look at the situation objectively when they made periodic assessments of populations. The most reliable reports are likely to be those from trappers and the Animals and Birds Act Rangers. Trappers, who clearly had better knowledge of koala and possum populations, but were also likely to be highly biased, often contradicted official statements of decline. Trappers generally emphasised the strength of populations, whereas government officials (e.g. police, stock inspectors, crown land rangers) frequently said that koalas and possums were uncommon or rare. The trappers had a vested interest in reporting high numbers as they were often intent on getting harvest seasons opened, so their estimates of numbers should be discounted to some extent because of this potential bias. Persons hoping for an open season may sometimes have overestimated the numbers or made exaggerated claims of mass mortality. Most other observers, however, almost certainly lacked the close contact with the animals that would give them sufficient skill to estimate status reliably. Because of the great difficulty in estimating population size in wild animals, particularly species as cryptic as the koala and the various species of possums, these accounts must be treated with caution and are likely to be underestimates.

Observers that had no interest in, or were opposed to, open seasons usually suggested the animals were scarce or present in very low numbers. Mr Thomas Foley, a member of the State Parliament, in 1922 implied that squatters deliberately misled government officials about population status because they were opposed to open seasons, and that stock inspectors' opinions of numbers (based on their contact with graziers) were therefore unreliable[3]. However, police supplied most reports for most years (Table 3), and it is likely that their reports may be more reliable than others (a) because they were involved in enforcing the law with regard to cyanide, spotlights and illegal take and possibly had more direct contact with trappers, and (b) because the squatters would have less influence over the police. Once fauna rangers were appointed after 1926, their estimates of the numbers of animals were probably more accurate as they should have had sufficient experience to evaluate more accurately the available evidence on status. Before 1920, most reports came from property owners/managers (Table 3). After 1920, most came from public servants, particularly police. There were usually few reports from trappers (Table 3). The most reliable evidence of presence comes from positive evidence rather than negative evidence, that is, reports of the presence of animals rather than their absence, due to the difficulty of non-expert observers detecting the presence of animals. The most reliable evidence of high abundance comes from accounts of large numbers of deaths during periods of mass mortality, and from the numbers killed in the harvests.

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[2] Queensland State Archives: Department of Agriculture and Stock. AGS/N350A file 09856, 1907. Letter from J.W. Davies, Pomona, 2/7/1907.

[3] Queensland State Archives: Department of Agriculture and Stock. AGS/J150 file 379. 1922. Notes on a deputation to the Minister for Agriculture, 21/4/1922.

The report data in this analysis are mainly used as positive evidence for factors such as population size, but not as negative evidence; that is, the absence of reports is not usually used to indicate absence of animals.

Results - *P. cinereus*

Health and disease

Historical accounts of disease and other health problems

Observations of disease and high levels of mortality formed a constant backdrop to the *P. cinereus* harvest. Disease, in conjunction with the harvest, gave rise to concerns about possible extinction, and questions about disease were built into the annual surveys of koala status carried out by the Department of Agriculture and Stock. The majority of disease reports came from the early to mid 1920s when stock inspectors, lands officers and police were queried concerning open seasons and animal numbers. Disease was widely reported and generated interest in the community and was sufficiently common to give rise to local and state-wide mythology about the nature of the disease and causes of mortality. Disease was commonly attributed to intestinal worms, over-population, hot weather or blowfly strike. It is likely that disease would not be noticeable unless symptoms were relatively visible, indicating that the disease had progressed to a point where it was having a severe effect on the animal and/or was affecting a large number of animals. Disease reports, therefore, may indicate severe infections in the population. Nearly all reports of disease were accompanied by reports of high levels of mortality.

Table 3. Number of reports of koala and possum status grouped by source for five-year periods.

	DPI	Forestry	Lands	Police	Property owner	Trapper	Other	Total
Koala								
1885-1890					1			**1**
1896-1900					1			**1**
1901-1905				1			2	**3**
1906-1910	1			1	2	1	1	**6**
1911-1915					2			**2**
1916-1920					3	2	1	**6**
1921-1925	97	19	76	343	3	8	5	**551**
1926-1930	30				9	5	12	**56**
1931-1935	3					1		**4**
1936-1940	1				1		2	**4**
1941-1945					1			**1**
Possum								**0**
1865-1870					1			**1**
1885-1890					1			**1**
1891-1895					2			**2**
1901-1905			1					**1**
1906-1910	2				1		1	**4**
1911-1915	8						1	**9**
1916-1920						1		**1**
1921-1925	82	18	68	314		4	4	**490**
1926-1930	23				1	1	2	**27**
1931-1935							1	**1**
1936-1940					1		3	**4**

Fletcher *et. al.* (1959) stated in a history of Ballandean that a sickness overtook koalas in the 1890s and they were often seen sitting at the foot of a tree too ill to climb. Koala disease was reported in the newspapers also. For example, in 1919, *The Brisbane Courier*[4] stated that, "Some eighteen months ago it was reported bears were falling dead from the trees but nothing more has been heard of this for some time so it is assumed the disease from which they were suffering has died down."

People were sufficiently interested in koala deaths to investigate the causes. In 1923, the police at Baralaba reported: "It is considered that this death-rate is not due to the bears becoming too numerous. A selector of this district has opened several dead bears, and found them to contain a mass of worms", implying that worms were the cause of death[5]. It was also observed that deaths attributed to disease or overpopulation might have easily been caused by koalas eating cyanide baits left behind by trappers. Accounts of disease and mortality were often used to bolster positions taken in other controversies. Overpopulation was used to support the case for having open seasons (so as to get the economic benefits from bears that were allegedly doomed to die anyway), whereas mortality from disease was used to argue against open seasons as bears were then supposed to be too scarce for a harvest. The supposed accidental poisoning of bears with cyanide was cited during attempts to prevent the use of cyanide for trapping possums.

The Courier-Mail, in an article entitled "Hope for the Koala"[6], reported, "A factor that might contribute to a material reduction in the number, however, was some mysterious malady that seemed to affect the koalas from time to time. Some years ago there was a fairly large bear population in a section of the desert country of Central Queensland. Then a mysterious disease broke out among them and the mortality must have been very great indeed. Old bushmen were of the opinion that it was not a disease that was responsible for their death, and pointed out that as the bears had not been molested for a number of years the available food supply was less than they required." (The desert country refers to the Desert Uplands Bioregion, Sattler and Williams 1999).

Disease symptoms in P. cinereus

Most of the symptoms reported match those of common diseases found in *P. cinereus* in Queensland today, including the chlamydial diseases cystitis ("dirty tail") and kerato-conjunctivitis ("pink-eye"), and a rhinitis-pneumonia condition (Carrick 1996). Examples of more detailed descriptions are shown in Table 4 and reported symptoms are summarised in Table 5. Disease was frequently attributed to worms in the intestine and most reports of disease were associated with the occurrence of high levels of mortality during hot dry weather. Diseases were also commonly attributed to infantile paralysis (i.e. poliomyelitis), distemper, pink-eye, blow-fly and pleurisy. Most of these conditions are likely to be chlamydial infections (Tables 4, 5).

Blowflies were reported commonly, possibly indicating that the sheep blowfly swarmed on *P. cinereus* with cystitis or conjunctivitis. The sheep blowfly is now scarce in inland regions due to the introduction of dung beetles, but was likely to have been common then.

Table 4. Descriptions of koala disease from observers in the early 20th century, with current interpretation. "Source" refers to source material below table.

Observer	Description	Interpretation	Source
H.J. Close, Rolleston, 26/2/1921	"The destruction bears from natural causes is greatly added to because of the bounteous rains & wonderful season. At present bears are dying of Pink Eye caused by worms Blow flies which affects the crutch as in sheep Pluro caused by the wet season. The lungs in some cases adhering to the ribs in others the lungs a mass of blubber & the cavity of chest full of fluid (virus)."	1. Kerato-conjunctivitis 2. Cystitis 3. Rhinitis-pneumonia	1
Stock Inspector R.J. O'Bryen, Toowoomba, 28/3/1923	"A disease known as rumpus or commonly called Mange – odd cases have been known in parts of this district."	Cystitis	2
Land Ranger R.S. Gibbings, Maryborough, 12/2/1923	"The disease is attributed to worms in the food canal (probably lower intestines). The symptoms are loss of size and condition, dry tight-drawn skin, thiner fur of less even length and darker in colour about the loins, where the lighter patch on the rump usually is, fur dung stained about the fundament and extending to the hips and thighs."	Cystitis	2
Police report, Rolleston, 1923	".... bears are seen dying in hundreds at different places, the cause is attributed to be pleurisy, "Pink Eye", and Fly Blow, by several persons who have examined the bodies."	1. Rhinitis-pneumonia 2. Kerato-conjunctivitis 3. Cystitis	3

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[4] *The Brisbane Courier,* 11/3/1919.

[5] Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Police report on open season, no date 1923.

[6] *The Courier-Mail,* 10/7/1934. Article: "Hope for the Koala".

Observer	Description	Interpretation	Source
Stock Inspector Tannock, Springsure	“Disease has been existent among native bears for many years, e.g. catarrhal fever or influenza, in many cases this assumed the form of pink eye in that the characteristic of which are conjunctivitis and swelling of the eyelids with a discharge of tears over the face, these excretions becoming purlent as the disease advances. The disease generally can be regarded simple or uncomplicated whilst in other instances pulmonic, gastro-enteric, hepatic and rheumatic complications occur. There frequently occurs a discharge from the nose which becomes flaky, thick, yellow and profuse in progress of the disease, analogous to snuffles in rabbits. ...... the region around the anus and vulva are constantly moist & give rise to foetid odour, & that the skin in consequence around that part of the anatomy takes a considerable time to dry. .... During the progress of the disease the hair falls out in patches, it is this and the discharges from the eyes and nose that are indicative of the existence of the disease to trappers. Stomach worms of Strongylus genus are prevalent in native bears more or less, especially during dry seasons, when it is thought these are accountable for a certain percentage of deaths .....”	1. Rhinitis-pneumonia 2. Kerato-conjunctivitis 3. Cystitis	4
Police report, Merinda, 1923	“A disease like a rash was noticed among the native bears of the district, especially among older bears.”	Unidentified	3
Stock Inspector Kidd, Juandah, 14/2/1923	“It is of course well known that a good few bears die after or during a long dry spell, the principal cause being worms, & when in such a state their skins are useless.”	Unidentified	2
Police report, Baralaba, 1923	“A disease has been noticed ... which is alleged to be due to scour and worm, and this disease has thinned them out to such an extent that it is not considered necessary to open a season during the current year. .... A selector of this district has opened several dead bears, and found them to contain a mass of worms.”	Cystitis	3
Stock Inspector Cardno, Miles, 5/2/1925	“A disease was noticed in the bears some three years ago in this district. .... The disease appeared to be similar to distemper in a dog, there being a discharge from the nose, eyes and anus.”	1. Rhinitis-pneumonia 2. Kerato-conjunctivitis 3. Cystitis	5
Land Ranger P. Smyth, Mackay, 27/1/1925	“In 1922-3, I marked a disease among Native Bears, which appeared to be akin to infantile paralysis in human beings, but the distemper appears to have run its course, and I did not observe any diseased Bears in 1924.”	Unidentified	6
Forest Overseer Keliher, Corella (Gympie), 12/2/1922	“... they are dopey and a kind of matter yellow in colour leaving their privates which gives a very strong smell, I believe it to be a veneral disease or abortion such as cattle and horses suffer from.”	Cystitis	7
Ranger G.P. Power, Rockhampton, 5/11/1930	“I have not had the opportunity yet to come across one on the ground with a disease, but I have seen them up the trees with worms.”	Cystitis	8

Sources:

1. Queensland State Archives: Department of Agriculture and Stock. AGS/J150. 1921. Letter from H.J. Close to T.A. Foley, 26/2/1921.
2. Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Summary of reports on open season, 26/3/1923.
3. Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Police report on open season, no date 1923.
4. Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Memo from Stock Inspector Tannock, Springsure, 14/2/1923.
5. Queensland State Archives: Department of Agriculture and Stock. AGS/J325 file 545. 1925. Memo from Stock Inspector Cardno, Miles, 5/2/1925.
6. Queensland State Archives: Department of Agriculture and Stock. AGS/J325 file 545. 1925. Memo from Land Ranger Smyth, 27/1/1925.
7. Queensland State Archives: Department of Agriculture and Stock. AGS/J150 file 379. 1922. Memo from Forest Overseer Keliher, Corella (Gympie), 12/2/1922.
8. Queensland State Archives: Department of Agriculture and Stock. AGS/J733 file 3604. 1930. Memo from Ranger Power, Rockhampton, 5/11/1930.

Accounts of "mange" are interpreted here from the context as cystitis. However, one report of a condition in which all fur left the body (Table 5) may refer to sarcoptic mange, said to be responsible for mass mortality of all bears on the Barcoo about 1903-1904[18]. Mange is uncommon in wild *P. cinereus* (Barker 1974; Wood 1978; Martin and Handasyde 1999). A report of mass mortality on the upper Burnett and Dawson in 1926 stated that *P. cinereus* died from a disease which left the fur absolutely valueless, depriving it of all lustre, and in most cases the hind quarters were mangy and devoid of fur[7]. This is thought to be an account of cystitis. A number of people complained that the fur of bears dying during episodes of mass mortality becomes valueless and of no use for harvesting. Poor fur condition, consisting of loss of guard hairs, has also been described in zoo *P. cinereus*, possibly due to poor nutrition (Gordon 1996), and some historical reports may be referring to this condition.

There were two reports of tick infestation, both from Wide Bay and Burnett District[18,8]. In 1925, the police at Pialba reported that koalas had died 10 months ago and were covered in cattle ticks, and ticks were sometimes blamed for deaths of koalas[8].

Accounts of paralysis and infantile paralysis (i.e. poliomyelitis) are interpreted here as general weakness present in *P. cinereus* that are so ill from other causes that they are unable to climb. However, paralysis might also refer to tick paralysis. One report (Land Ranger Smyth, Table 4) associates infantile paralysis with symptoms of chlamydial infection, i.e. "distemper".

Many observers reported that an unspecified disease was present, or attributed mortality to the presence of intestinal worms. It is possible that much of this mortality was due to other causes, and did not involve disease, as other plausible causes were apparent, such as deterioration of the food supply. The reports that are most likely to be genuine records of the presence of disease are those that include symptoms (Tables 5, 6). Reports of intestinal worms presumably refer to the cestode *Bertiella obesa* (Spratt 1978; Wood 1978). It is clear that heavy worm infestations occurred commonly, possibly building up in animals that were weak from other

Table 5. Disease symptoms in koalas described by observers in the early 20th century, with current interpretation.

Symptom	Interpretation
Distemper, Non-fatal disease resembling distemper	Chlamydial infection, not identified further. Canine distemper may include a discharge from eyes, nose, anus.
Pink-eye	Conjunctivitis
Blow-fly, Fly-blow, Sheep-fly	Cystitis
Scabby ulcerous disease, Disease of ulcerated nature	Cystitis
Venereal disease	Cystitis
Scour, discharge from cloaca	Cystitis
"rumper disease", "rumpus", "mangy rump" or "mange"	Cystitis. Some occurrences may be sarcoptic mange, but mange is mainly a disease of captive koalas and not normally conspicuous to a lay observer.
Pleurisy, Pleuro	Rhinitis-pneumonia
Skin disease	Cystitis
Influenza	Rhinitis-pneumonia
Tubercle	Lung infection - Rhinitis-pneumonia
Paralysis, infantile paralysis [= poliomyelitis], paralysis disease	Unidentified. Apparently refers to weak animals, e.g. too weak to climb trees, and thought to have paralysis, or paralysis of hindquarters. Many diseases (and other conditions) could result in apparent weakness. Might be tick paralysis, but appears to be too common – tick paralysis would be expected to be less common.
A disease in which all fur left the body	Unidentified (possibly sarcoptic mange?)
Disease like a rash	Unidentified
Lungworm	Unidentified. Possibly confused with intestinal worms.
Worms	Unidentified, or no disease present. Probably includes cystitis, as it may have been associated with presence of worms, or worms may have been associated with loss of fluid from cloaca. Observers appeared to associate 'Scour' and cloacal discharge with worms.
Tick infestation	Two reports found.

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[7] *The Queenslander,* 28/7/1927. Article: "Native Bear and Opossum, possibility of extinction".

[8] Queensland State Archives: Department of Agriculture and Stock. AGS/J325 file 545. 1925. Memo from Constable Heaney, Pialba Station, 3/2/1925.

Table 6. Number of reports of diseases and other conditions in koalas in each Opossum District over the period 1890-1935. Approximately ninety per cent of reports are from 1920-27. 'Ex District' indicates records from rest of State, west of the Opossum Districts.

Disease	Central Coast	Central West	Darling Downs	Moreton	Northern	North Coast	South-Western	Wide Bay Burnett	Ex District
Cystitis	5	4	1	1			1	2	
Kerato-conjunctivitis		1				1	3	1	
Conjunctivitis/ cystitis/rhinitis		6							
Chlamydial infection (unidentified)			2			1		2	
Rhinitis-pneumonia	2	1							
Tick infestation									
Worm infestation	15	6	4	1			10	2	
Unidentified disease	8	6	5			9	7	3	3
Total	**30**	**24**	**12**	**2**		**11**	**21**	**12**	**3**

causes. However, Spratt (1978) implies that *B. obesa* may also have a serious impact on the host. A report from Samsonvale referred to a disease caused by a lungworm, said to have been responsible for a disastrous koala decline (Table 5) (Smith 1988). This may have been confused with intestinal worms. The context of some reports indicates that some, or possibly many, accounts of "worms" referred to cystitis. For example, Ranger Power (Table 4) reported seeing bears in trees with worms. As no worms would be visible in such a situation, the symptoms seen were probably those of cloacal discharge from cystitis. Police at Baralaba (Table 4) associated "scour" (= cystitis) with "worm". See also the report by Land Ranger Gibbings (Table 4). Apparently, the observation of worms in the intestine was associated causally with the discharge from the cloaca characteristic of cystitis.

Occurrence of disease in P. cinereus

P. cinereus diseases were reported in all Opossum Districts except Northern District (Table 6). Variation in the total number of reports between Districts is related partly to *P. cinereus* status as well as differences in occurrence of disease. It is likely that more reports were generated where *P. cinereus* was most abundant, and therefore visible to observers, and where there was most human interaction with *P. cinereus* (i.e. harvesting). The number of reports was lowest in Moreton and Northern, and highest in Central West, Central Coast and South-western Districts. The low number of disease reports in the Northern District probably reflects both the low populations of *P. cinereus* and less human interaction with *P. cinereus* (both population size and hunting were much lower in that District). In Moreton, *P. cinereus* numbers were low for much of the period covered by the reports. However, it is also possible that low density populations had lower incidence of infectious disease.

Chlamydial diseases occurred in most Opossum Districts, and in central, southern, coastal and inland areas of the State, but were low in the north (Table 6). Cystitis was reported most commonly (14 reports, 6 Districts), whereas conjunctivitis had six reports from four Districts. Most reports of chlamydial disease came from the Central West District (Table 6). Chlamydial diseases persisted over a number of years in some Districts.

P. cinereus mortality

Observers reported few to many deaths. Reports indicating high levels of mortality (Table 7) were collated, and used to compile information on mortality per Opossum District per annum (Table 8). Examples of statements showing evidence of mortality are shown in Table 7. Many observers reported that *P. cinereus* mortality had occurred recently or at earlier times. Reports include both high and low levels of mortality, but mainly the former as far as the extent can be assessed from the reports (Table 7). The reports indicate times when the level of mortality was high enough to be visible to lay observers. Such reports are interpreted here as evidence of very high levels of mortality and probable severe declines in population size, as low levels of mortality would not be easily visible to casual observers.

The number of reports is higher in inland Districts than in coastal Districts on the same latitude (Central Coast v Central West; and Moreton v Darling Downs v South-western) (Table 8). Reports are also higher in central Queensland than in most southern and northern Queensland Districts. The number of reports is low in the Moreton and Northern Districts and relatively high elsewhere, with most reports coming from Central West, followed by Central Coast and South-western Districts (Table 8). The high number of reports in the Central West District probably reflects high abundance in a semi-arid climate where environmental pressures are higher. The proportion of mortality reports per District is mostly similar to the proportion of disease reports per District (compare Tables 6 and 8).

Observers often commented on the cause of high levels of mortality. Their comments are clearly speculative and written without any specialist knowledge of wildlife ecology and sometimes with little basis in evidence. Stated causes included: worms, unidentified disease, over-abundant populations (usually when encountering hot dry weather, and possibly with failure of food supply), diseases (as listed above), drought, gales, cyclone (cyclone at Sarina, 1918), bush fire, dingo predation, fox predation, pear scrubs and eating fruit of the pear.

Table 7. Examples of reports of koala mortality found in departmental files and elsewhere, and their interpretation as indicators of high or low levels of mortality. "Source" refers to source material below table.

Report	Statement	Source
Interpreted as low level mortality, or uncertain		
H.R David, Assessing Ranger, Rockhampton, 17/2/1923	"... have noticed odd bears dead but could not account for it, except the excessive heat and dry weather."	1
Stock Inspector Kidd, Juandah, 7/2/1925	"I have only heard of 3 dead bears being seen this season. Deaths having been attributed to worms."	2
Ranger Hunter, Roma, 22/1/1925	"I have noticed an odd dead bear at times, but these are very few indeed."	3
Interpreted as high level mortality		
Police report on open season, Banana, 1923	"A great number of bears died from disease in this District during 1922, but the cause for their death could not be ascertained"	4
Police report on open season, Capella, 1923	"During the past two years a number of bears have died in the District, but there has been no disease among them. A severe bush fire passed through the District last October and November, killing a number of them."	4
Mr Triffit, Barwon Park, Central West District, 30/1/1923	"... countless thousands of Bears ... died during the summer months of last year 1922 through disease, caused I believe through their being to many. I have seen from 10 to 15 dead in one day at the foot of the gum trees."	5
Police report on open season, Marian, 1923	"Native Bears have been seen lying dead in places, under trees, but not to any great extent. It is thought that these bears died from the excessive heat which has been experienced in this district lately."	4
Land Ranger R.S. Gibbings, Maryborough, 12/2/1923	"... native bears are subject to disease, and a large number die annually from this cause. I am inclined to the belief that there was a heavier mortality last Spring than usual."	6
Land Ranger Kelly, Duaringa, report on open season 11/3/1924	"Dry weather and heat caused a large number of deaths among native bears."	7
Police Sergeant Cahalane, Springsure, 8/2/1924	"Native Bears are said to be fairly plentiful, the recent dry weather and excessive heat was responsible for some deaths amongst them."	8
Police Sergeant Hanrahan, Banana, 25/1/1925	"A great number of bears died and in parts of the district are still to be seen dead from some disease but I cannot give any cause."	9

Sources:

1. Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Memo from H.R David, Assessing Ranger, Rockhampton, 17/2/1923.
2. Queensland State Archives: Department of Agriculture and Stock. AGS/J325 file 545. 1925. Memo from Stock Inspector Kidd, Juandah, 7/2/1925.
3. Queensland State Archives: Department of Agriculture and Stock. AGS/J325 file 545. 1925. Memo from Land Ranger Hunter, Roma, 22/1/1925.
4. Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Police report on open season, no date 1923.
5. Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Letter from R.H. Triffitt of Barwon Park Station, 30/1/1923.
6. Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Summary of reports on open season, 26/3/1923.
7. Queensland State Archives: Department of Agriculture and Stock. AGS/J262 file 2003. 1924. Summary of reports on open season, 11/3/1924.
8. Queensland State Archives: Department of Agriculture and Stock. AGS/J262 file 2003. 1924. Memo from Police Sergeant Cahalane, Springsure, 8/2/1924.
9. Queensland State Archives: Department of Agriculture and Stock. AGS/J325 file 545. 1925. Memo from Police Sergeant Hanrahan, Banana, 25/1/1925.

Robbie Goody reported that, in the Monto region, "… shortly after 1927, the bears contracted a disease and died in hundreds. You would find them at the foot of trees too weak to climb" (Johnston 1982). Koalas virtually died out in the Springsure area in the 1920s, apparently from chlamydial disease (Rolfe 2001). Rolfe's grandfather, born in 1900, reported that, "... thousands of bears died … between the years 1923 to 1929 from a disease known … as 'Pink Eye'. The disease, not the man with the gun, practically exterminated this little animal from the Central West through to the east coast…. This was a cruel disease; they contracted the blindness then the urinal disorder, to finally die at the butt of trees after lingering for up to six weeks. They died not only along the rivers and creeks, but back in the range country. … I never saw one koala in any type of country in the West for forty five years" (Rolfe 2001). According to Rolfe, koalas were not seen again in this District until the 1960s, becoming increasingly common through the 1970s and 1980s.

Table 8. Number of reports of koala mortality per Opossum District per year. 'Ex District' indicates records from the rest of the State, west of the Opossum Districts.

Year	Central Coast	Central West	Darling Downs	Moreton	Northern	Northern Coast	South-western	Wide Bay Burnett	Ex District
1890			1						
1893	1								
1900			1				1		
1903							3		2
1904							1		
1910							1		
1916			2						
1918						1			
1919		1							
1920									
1921		2						1	
1922	1	6				2	1	1	
1923	2	9	1			6	8	1	
1924	6	9	1		1		5	3	
1925	4	5				1	3		
1926	2	3							
1927	1	1				1			
1928								1	
1930						1			
1932						1			
1935						1			
Total	**17**	**36**	**6**	**0**	**1**	**13**	**20**	**7**	**2**

Prickly pears, consisting of several species of the cactus *Opuntia*, were serious invasive weeds in the early 20th century, occurring in much koala habitat. We have only found brief references to prickly pear, which was said, by different observers, to be either harmful or beneficial to bears and possums. It is not clear what impact, if any, it had on their numbers. One Ranger reported that pear scrubs protected bears and possums from trappers, presumably due to difficulty of gaining access into such areas. Ranger Williams wrote that, "The prickly pear country has always been a great protection for both Native Bears and opossums, and they usually seem plentiful near by scrubs especially when the scrub is pear infested"[9]. Another correspondent stated that poisoning of prickly pear would harm possums[10], and eating the fruit was said to be harmful. In 1923, the Sub-inspector of Police at the Jackson Police Station in the Roma District observed that the country was thickly infested with prickly pear, and he considered that it was responsible for the disappearance of native bears[5].

Bushfire was mentioned several times in the early 1920s as a cause of mortality (at Rolleston, Capella, Charters Towers and Taroom) [5,18,11,12]. This is not a prominent cause of mortality in Queensland now. Heinsohn (1973) reported a fire on Magnetic Island, near Townsville, that was thought to kill more than half of the koala population in 1972. Mortality from cyclones and gales was also mentioned (one report of each [5,18]).

When climatic conditions are given, reports by observers almost always stated that mortality occurred in hot weather, i.e. in summer, during dry periods. There is only one report stating that mortality occurred in winter. Mortality was frequently linked to high numbers or drought. A report by police from Springsure in 1923 noted that, "For many years Native Bears have been noticed to die when the seasons have been favourable for good food. They become mangy and emaciated and die. The disease among bears is attributed to their being too numerous and to heat. When bears have been thinned out in open seasons it has been noticed that those remaining appear far healthier than previous to the season"[5]. Senior Sergeant Cahalane, Police, Springsure, reported, "It has been noticed that many Bears die from time to time, especially in hot weather, the deaths are attributed mostly to worms which cause the bears to become sick and they are unable to climb the trees, and die or are killed by dingoes; others have noticed Bears get mangey around the rump, become poor and fall off the trees, this is noticed mostly amongst the old animals; the general opinion is that a thinning out would improve the Bears"[13]. In 1924, Cahalane reported that the Aboriginals "consider that deaths are due to the gum trees being too dry and not sufficient fresh soft feed" [14]. Mr McDonald, the Charleville Assessing Land Commissioner, also noted in 1923 that koalas may die during drought from lack of young leaves on the trees [1]. Stock Inspector Kidd, Juandah, reported, "It is of course well known that a good few bears die after or during a long dry spell, the principal cause being worms, & when in such a state their skins are useless"[1].

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[9] AGS/J733 file 3604. Memo from Ranger A.K. Williams, 5/11/1930.

[10] AGS/J201 file 2003, 1923. Letter from J. Maguire, Miles, 7/5/1923.

[11] Queensland State Archives: Department of Agriculture and Stock. AGS/J150. 1921. Letter from H.J. Close to T.A. Foley, 26/2/1921.

[12] Queensland State Archives: Department of Agriculture and Stock. AGS/J325 file 545. 1925. Memo from A/Sergeant Adams, 2/2/1925.

Observers often stated or implied that populations went through a cycle where they built up to excessive levels during good seasons, and then died back severely when they next encountered a hot dry summer, with death sometimes attributed to deterioration of the food supply, and often to intestinal worms. Mr Dendle, Ranger Springsure, in a memo to the Under Secretary Department of Agriculture and Stock in 1927 wrote, "I myself am not opposed to both [i.e. koala and possum] seasons opening as my experience has been that if bears are left alone they will breed so thick that eventually a disease will break out among them and practically wipe them out which has been the case in this District" [15]. This pattern of population increase and decline is consistent with a description by Gordon *et al.* (1988) of a *P. cinereus* population crash in 1979-1980 during a hot dry summer at Mungalalla Creek in south-western Queensland.

It is not generally clear from reports if high levels of mortality recurred in the same population in successive years. Some reports indicate that this did happen within Opossum Districts at least, if not within local populations. For example, a petition from trappers from Springsure in 1919 stated, "in this and Rolleston district they die in hundreds every year" [16]. Land Ranger Leggett, Emerald, wrote in 1923, "at different times of every year I have noticed a good quantity dead at the foot of trees" [17]. Land Ranger Gibbings, Maryborough, reported in 1923, "native bears are subject to disease and a large number die annually from this cause" [1]. However, most reports imply that high mortality occurred at intervals of a number of years.

Some reports also indicate that mortality did not always occur in synchrony between Opossum Districts, and even local centres. In 1923, Stock Inspector Kidd, Juandah, reported "I have heard the rumour they [koalas] were dying by thousands in some places. I have never come on a dead one myself though traveling in the bush constantly" [1].

P. cinereus population size

Historical accounts of population size

Koalas were abundant in the Ballandean area in the 1890s. George Smith took 1,397 koalas in three and a half months in 1896, equivalent to about 13 per day (Fletcher *et al.* 1959). Native bear populations became greatly depleted at Ballandean by the turn of the century and did not recover. In 1922, Mr G. Mundell stated that in 1902 they used to shoot bears on the Condamine River country and get about 100 in one day. He himself had shot 50 in a day [3]. Police at Miles on the western Darling Downs reported in 1924 that bears had been very scarce since the 1902 drought [18].

The regular official reports on status that commenced in 1922 occasionally included information on numbers seen and population changes. Police at Hungerford in 1923 [5] reported that no native bears were present and stated that it was believed bears died during the big drought (c. 1895-1903, Bureau of Meteorology 1989). In the same year, Condamine police reported that no bears were present and stated that none had been seen for the past four years.[5] Charters Towers police in 1923 reported that no bears had been seen for five and a half years [5]. A Land Ranger in Toowoomba in 1923 said he had only seen three bears in the last 10 years in the Inglewood district [1]. Bollon police in 1925 stated that none had been seen in the past nine years up to 93 miles from town, but they were plentiful 15 years ago when they suddenly died out from an unknown disease, "as they were often found at the foot of trees, unable to climb, though the season was from fair to good"[19].

In August 1928, the Nature Lovers League (a young person's section of the Queensland Naturalists' Club) surveyed koala status by writing to Shire Councils, Dingo Boards and municipal Councils with questions on the status of native bears, and asking if they were in favour of protection. Three shires reported bears plentiful;

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[13] Queensland State Archives: Department of Agriculture and Stock. AGS/J325 file 545. 1925. Memo from Sergeant Cahalane, Police Springsure, 22/1/1925.

[14] Queensland State Archives: Department of Agriculture and Stock. AGS/J262 file 2003. 1924. Memo from Police Sergeant Cahalane, Springsure, 8/2/1924.

[15] Queensland State Archives: Department of Agriculture and Stock. AGS/J463 file 2455. 1927. Memo from Ranger Dendle, Springsure, 10/5/1927.

[16] Queensland State Archives: Department of Agriculture and Stock. AGS/J104 file 1826. 1927. Petition from trappers, Springsure, 25/1/1919.

[17] Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Memo from Land Ranger Leggett, 19/2/1923.

[18] Queensland State Archives: Department of Agriculture and Stock. AGS/J262 file 2003. 1924. Summary of reports on open season, 11/3/1924.

[19] Queensland State Archives: Department of Agriculture and Stock. AGS/J325 file 545B. 1925. Memo from Constable Adams, Bollon Station, 20/1/1925.

69 shires - eliminated or very scarce; 2 shires - no bears seen since the open season; 7 shires - no information on numbers; and 21 shires - no bears in the district [20].

Mr Rolleston reported that koalas were still abundant in the Northern Coast District in 1928 following the last open season (in August 1927), stating that hundreds were to be seen and on one occasion, he counted 10 in one tree [21]. In the mid 1930s, koalas were struck by illness and found with eyes "gummed" up at the foot of trees, too weak to climb. Following this they were absent from the region, even though their former habitat remained.

In 1930, Mr Power, the Ranger from Rockhampton, reported that native bears, although not numerous elsewhere, were "very thick" (he counted more than 20 bears in one day riding on horseback) on Clive and Yattan and along the Isaac [22]. The Ranger reported koalas to be plentiful in 1934 on Curtis Island [23]. In 1936, Mr Sutton wrote, concerning the area around Warwick and Wallangarra, that koalas were totally extinct where years ago they were plentiful [24]. At the same time, Mr H.E. Hiron of Raglan stated he had lived in the bush for 40 years and had not seen a single koala in 12 months where one time you could see dozens in one day [25].

However, in 1934, Animals and Birds Act Rangers suggested that koala numbers were not declining [6], and in 1936, officials of the Department of Agriculture and Stock were inclined to believe that the bear population must still number hundreds of thousands[26]. Given the often pessimistic official reports of koala status during the 1920s, these positive reports in the 1930s are unlikely to be over-stating koala status. These reports correlate with good status in central Queensland during the 1930s (see below).

Population trends

Observers' opinions of population numbers indicate that *P. cinereus* populations in southern and central Queensland showed pronounced fluctuation in size from the late 19th century into the early 20th century. Population size in southern Queensland (Moreton, Darling Downs and South-western Districts, Figure 3) was high in the late 19th century and fell in the early 20th (note, however, that sample sizes are low for this period, Table 3). Populations in Wide Bay and Burnett District declined into the 1920s, a later decline than in Districts farther south. Moreton District showed signs of an increase again in the late 1920s.

In central Districts (Central Coast, Central West and Northern Coast), population size was high in the early to mid-1930s (Figure 3). It was probably low before that in the 1900s, expanding in the late 1910s, and declining in the 1930s. In the Northern District, in contrast to other areas, there is no evidence of pronounced fluctuation or high abundance, with a small decline from 1919 to 1930 (Figure 3).

The fluctuation in numbers varies broadly with latitude, although Districts within similar latitudes do show some differences in timing of population fluctuations. The most southern Districts had high numbers early in the period and low numbers later (Moreton, Darling Downs and South-western) (Figure 3). Wide Bay and Burnett District shows fluctuations slightly later. The central Districts show high numbers in the mid to late 1920s and the Northern District probably failed to undergo severe fluctuations (Figure 3).

Table 9. Estimated status of koalas in April 1929, Northern, Northern Coast and Wide Bay and Burnett Opossum Districts, showing area of District in each status category. Data from Ranger W.E. Black, Department of Agriculture and Stock. "No. shires" shows number of shires in each category per District. "0" shires under the category "Plentiful" for Northern Coast indicates that only part of a shire fell into this category. Source: Queensland State Archives: Department of Agriculture and Stock. AGS/J565 file 604. Memo from Ranger Black, 12/4/1929.

District		Area (s. km) and Number of shires			
		Plentiful	Fairly Plentiful	Scarce	None
Northern	Area			29,017	330,114
	No. shires			1	16
Northern Coast	Area	2,590	32,410	29,048	
	No. shires	0	3	5	
Wide Bay Burnett	Area			60,842	13,672
	No. shires			10	7

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[20] Queensland State Archives: Department of Agriculture and Stock. AGS/J565 file 29/604. 12. Letter from D.A. Herbert, Nature Lovers League, 25/2/1929.

[21] *The Sunday Mail,* 25/10/1992. Letter from Mr F. Rolleston.

[22] Queensland State Archives: Department of Agriculture and Stock. AGS/J733 file 3604. 1930. Memo from Ranger Power, Rockhampton, 5/11/1930.

[23] Queensland State Archives: Department of Agriculture and Stock. AGS/J956 file 17303. 1934. Memo from Ranger Williams Rockhampton, 30/7/1934.

[24] Queensland State Archives: Department of Agriculture and Stock. AGS/J1079 file 3760. 1936. Letter from E. Sutton, 11/5/1936.

[25] Queensland State Archives: Department of Agriculture and Stock. AGS/J1079 file 3760. 1936. Letter from Mr H.E. Hiron, Raglan, 11/5/1936.

[26] *Telegraph,* 19/6/1936. Article: "May there never be another open season for bears".

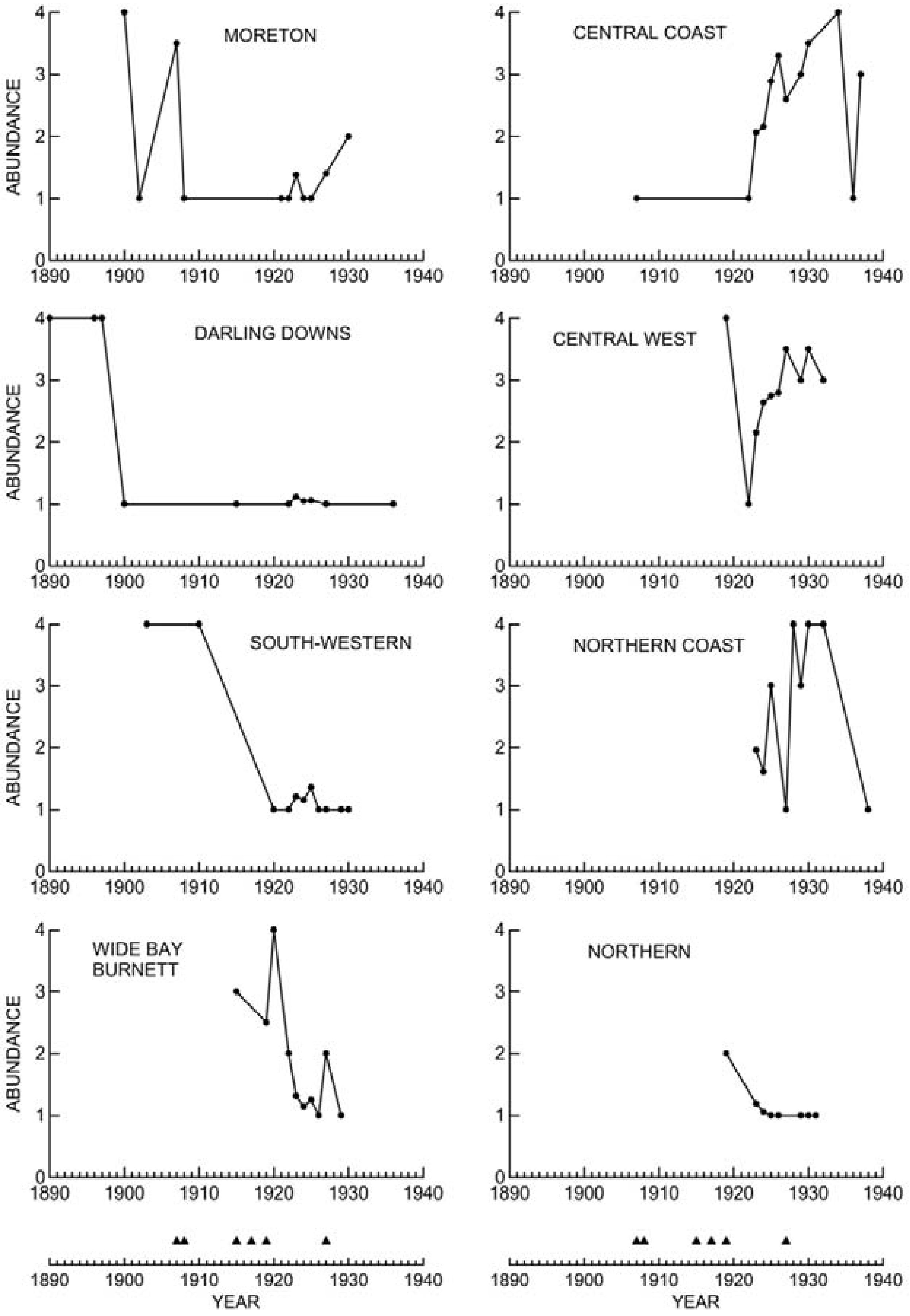

Figure 3. Records of koala numbers from 1890-1940. Symbols show mean status ranked in four categories, from scarce, 1, to abundant, 4. Solid triangles denote harvest years.

In 1929, Ranger W.E. Black gave detailed estimates of koala and possum numbers for each shire in the Northern, Northern Coast and Wide Bay and Burnett Opossum Districts, showing the number of square miles in each shire in each status category (Table 9). According to Black, koalas were common to abundant (fairly plentiful to plentiful) in about 55% of Northern Coast District, but scarce or absent in all of Northern District and all of Wide Bay and Burnett District.

Population size at the time of the harvests is unknown. However, there is evidence that population size was substantially higher during at least part of the harvest period. The evidence for high populations includes reports of visible mass mortality, reports of sightings of very large numbers of animals per day, and reports of high take per day. The strongest evidence of high numbers comes from observations of mass mortality. High levels of visible mortality can only occur when abundance is high, and the reports of mortality (Table 8) therefore provide additional evidence of periods of high numbers. Since high abundance does not always lead to high levels of mortality, and since mortality may not always be reported, the absence of reports does not indicate low population size. These reports are so widespread as to indicate that the total State population size was much higher for at least part of that period than it has been more recently. Over about three decades from 1971-2002, the Queensland Parks and Wildlife Service received only one report of high levels of mortality, at Mungalalla Creek in South-western District in 1979-1980 (Gordon *et al.* 1988), leading to the conclusion that koalas are much less numerous now than in the early 20th century. The reports of mass mortality also continue after the last open season in 1927, indicating that populations were still high in some areas after the harvest ended (Table 8).

In addition, a number of statements are available of observers sighting or taking large numbers of koalas in a single day. This kind of observation is unusual now in Queensland and indicates that koalas were common to abundant in those areas. There are also many reports to the contrary, stating that koalas were rarely sighted over lengthy periods. Although this is negative evidence and may come from inexperienced observers, the accounts are so common that it may be concluded that they are credible, indicating that regional population size was volatile, and that populations were at very low levels in some areas for at least part of the time.

Other evidence of status comes from the size of the harvest. If State-wide *P. cinereus* populations had declined substantially, it is unlikely that harvests of approximately 500,000 *P. cinereus* per season (Hrdina and Gordon 2004) would have been achieved. A high base population must have been present to permit a harvest of that size, at least up until the final harvest in 1927, following which populations were still expanding in central Queensland (Figure 3). The larger area of eucalypt forest and woodland present in 1906-1927 than now, also implies that populations were larger during that period, and could potentially support a high harvest. Wells *et al.* 1984 (cited in Pahl *et al.* 1990) reported that 44-47% of tall and medium forests with more than 10% canopy cover had been cleared in Queensland since European settlement. Finally, the wide distribution of the *P. cinereus* today (Kikkawa and Walter 1968; Campbell and McRae 1979; Patterson 1996) indicates that *P. cinereus* was not totally eradicated over large regions by the harvest, as it is unlikely populations could have declined and recovered again to reach their present extent. They may however, have been reduced to small local nucleus populations that later recovered and expanded locally.

Mortality reports show that numbers were high in Central West, Central Coast and South-western Districts during the 1920s (Table 8). The results for the latter District, however, conflict with the results from survey reports, which show low numbers (Figure 3). There were also high numbers in South-western District around the turn of the century. There is a smaller number of reports of mortality in Darling Downs, Wide Bay and Burnett and Northern Coast Districts in the 1920s. There is no evidence from the reports of high numbers in Northern District. Areas north of Townsville generally report no or very few koalas and few opossums (Figure 3, Table 8). In 1934, W.E. Black, Ranger Mackay stated (erroneously) that "the Native Bear is not found any further [sic] north than the Railway Line from Townsville to Hughenden" [27]. (Koalas have been found much farther north than this, to the vicinity of Cooktown (Patterson 1996).)

Reports also indicated that numbers varied substantially within each Opossum District. Mr Black reported different numbers between shires in the Opossum Districts shown in Table 9. Many other reports indicated differences in numbers between localities within Districts.

Trends in numbers do not show a consistent correlation with harvest periods, with some Districts showing a decrease, and others showing an increase. Following the exceptionally large 1919 harvest of nearly one million bears, there were probably declines in numbers in South-western, Wide Bay and Burnett, Central West and Northern Districts (Figure 3), although sample sizes (i.e. number of reports, Table 3) are small. However, this fall also correlates with major drought from 1918-20 (Bureau of Meteorology 1989, Figure 4). After the 1927 harvest of about half a million koalas, numbers increased in Central Coast, Moreton and Northern Coast Districts, and remained stable in Central West District. Population declines in Moreton and Darling Downs Districts at the end of the 19th century and in the first decade of the 20th century may correlate with the unregulated harvests that took place up until 1906. However, there is no information on the location, size and timing of these harvests.

Drought also fails to provide a consistent correlation with population trends. For example, drought in the late 1920s and early 1930s in Central West District is associated with high koala populations (Figures 3, 4). Observers attributed the declines to various factors, including the causes of mortality listed above, together with clearing of habitat, prickly pear and over-harvesting.

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[27] Queensland State Archives: Department of Agriculture and Stock. AGS/J956 file 17303. 1934. Memo from Ranger Black, 20/7/1934.

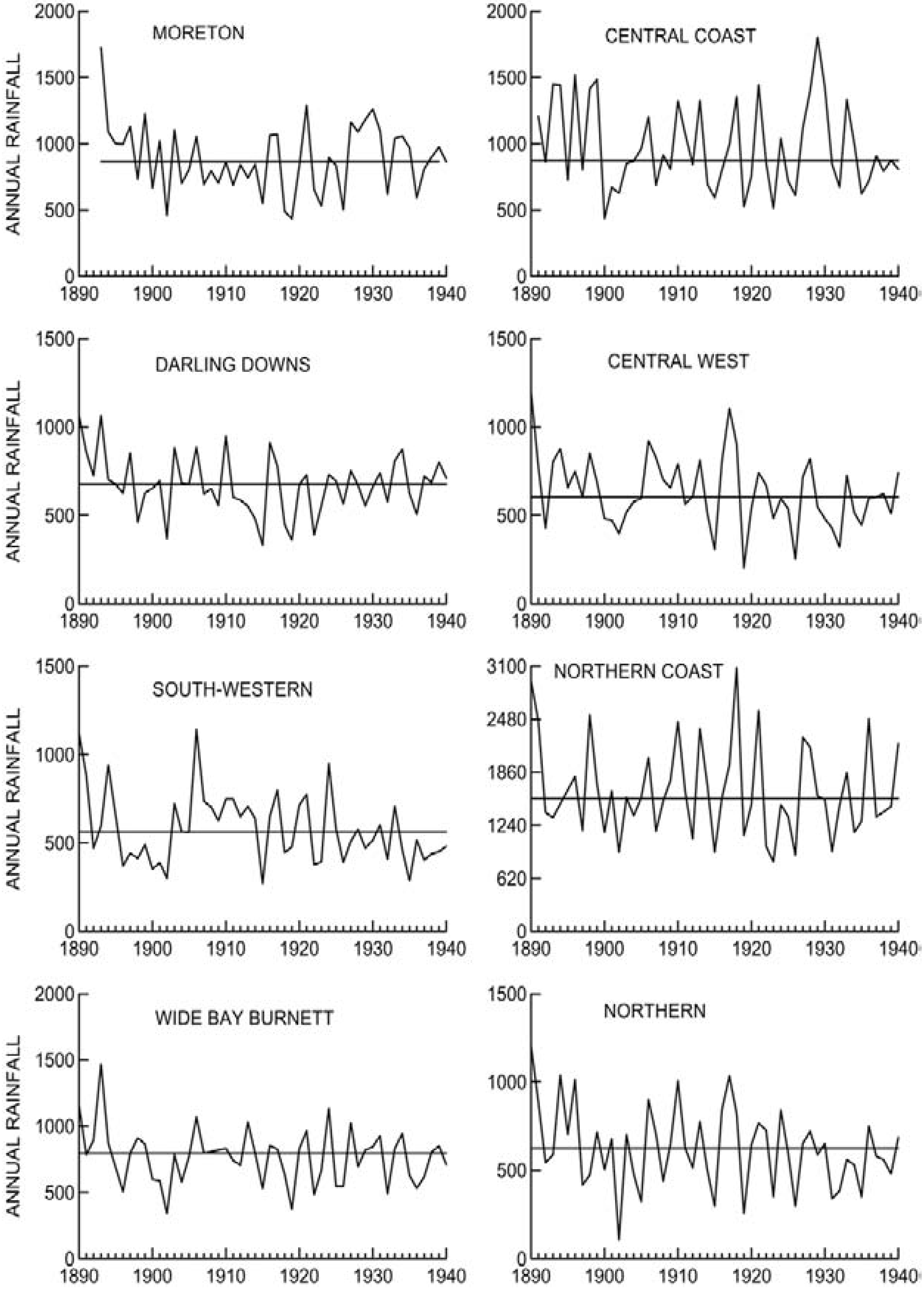

Figure 4. Annual rainfall at representative centres in each Opossum District, 1890-1940. Horizontal line shows median annual rainfall over the period. Stations are: Beaudesert (Moreton), Dalby (Darling Downs), Mitchell (South-western), Gayndah (Wide Bay and Burnett), Rockhampton (Central Coast), Emerald (Central West), Mackay (Northern Coast) and Charters Towers (Northern).

Results - possums

Historical accounts of possum status

Although a number of phalangerid species were harvested, most accounts in this section almost certainly refer to the Common Brushtail Possum *Trichosurus vulpecula* (Hrdina and Gordon 2004). Possums were very common in at least parts of Queensland at the end of the 19th century. Possums were numerous at Ballandean Station near Stanthorpe in the late 1860s to such an extent that they were pests on lucerne crops. In the 1888 drought, the same lucerne crop was teeming with possums, which were chased on the ground and killed with sticks (Fletcher *et al.* 1959). In 1894, the three Smith brothers snared 7,390 possums in four months and four days. This is equivalent to approximately 20 possums per person per day (Fletcher *et al.* 1959). Near St George in southern Queensland, possums increased in numbers after 1881 and declined severely by 1896 (Kerle 2001).

During the first 40 days of the 1908 season, Mr J. Guilfoyle of Beaudesert was reported to take 10,000 possum skins [28]. This implies an average harvesting rate of about 250 possums per day. It is inconceivable that one person could trap possums at such a high rate and it may be assumed that some of these skins were taken out of season or the trapper employed a team of workers. In 1909 at Rolleston, it was said that an average night's possum take per trapper "is about 50, and in good country the number is 100"[29].

As in the case of koalas, possum status was also the subject of official concern. In the debate on the 1906 Act, it was stated that "the farmer and his sons" had wiped out the opossum in many districts and in Dalby and Warwick they were practically exterminated (Queensland Hansard 1906). As early as 1911, an inquiry was made into the status of possums [30], apparently based on sending letters to district officers in the Department of Agriculture and Stock. The replies indicated that possums had become very scarce, or even "commercially extinct" in southern Queensland, but were more common farther north. It was felt that under existing conditions possums would soon become practically extinct. Some replies indicated that extinction would be delayed if snaring and shooting only were allowed and the use of cyanide was absolutely stopped. The effect of closer settlement on possum numbers was also commented on in the Annual Report, which stated, "It will be noted, further, that the progress of settlement in itself seems to diminish the numbers of opossums." The report concluded that definite action was needed if the possum was to be preserved in Queensland

By the 1920s, observers regarded possums as scarce in south-western Queensland, whereas they were common in central Queensland. In 1923, Mr MacDonald, Assessing Commissioner in Charleville, remarked that it was rare to see or hear an opossum on the Maranoa, Warrego, Paroo, Bulloo or Cooper Rivers or any western creek where they once were in thousands [1]. He felt that when cyanide came into general use about 20 years earlier (i.e. about 1903) they were "wiped clean out".

There was evidence of high possum abundance in fruit and cotton growing areas near Rockhampton and possibly other areas as possums were considered to be great pests in these areas [31]. Marshall Goody at Monto admitted to having taken 68 dozen possum skins before the 1926 possum season opened (Johnston 1982). He also stated that three men shot 219 possums before 1 am on the first night, i.e. 73 possums per person (Johnston 1982), indicating very high numbers. *The Queenslander* reported that it was common for trappers to take 50-100 opossums per night in 1926, although the take commonly diminished to about six per night by the end of the season [7].

In 1930, Mr Power, Ranger, Rockhampton, reported that opossum tracks were "thick" on the trees and there were also a lot of pads leading to water in the region of the Fitzroy and Mackenzie Rivers west of Rockhampton [22]. A letter to *The Courier-Mail* from a correspondent in Rockhampton in 1936 stated that, "one man shot 108 possums last night, and three others had shot 76 between them by 11 o'clock, in the same paddock and on the same night". This was about one month before the season opened [32]. Such high possum abundance is unknown now, and this level of harvest would be impossible to attain anywhere in Queensland today. (Densities in mainland Australia now are about 0.2-4 per ha, How and Kerle 1995.) In 1936, Mr Hiron of Raglan suggested that creeks and an area at least three miles (i.e. about five kilometres) on either side should be closed to possum trapping as these areas were the only places large numbers of possums were still found [25]. He observed that ring-barking had now restricted possums to the permanently watered creeks and rough back country in the hills.

Possum population trends

Information on possum disease and mortality is very sparse, in contrast to the situation for *P. cinereus*. Disease in possums was seldom commented on, and this information was not requested in government enquiries about opening seasons. In 1923, Mr Ford, Stock Inspector at Richmond, reported that locals believed that a disease "wiped out" possums there about eight years earlier and Mr Arnold, the Assessing Commissioner in Rockhampton commented that a disease was credited with "exterminating" possums on the Lower Warrego years ago[1]. (The Assessing Commissioner, Charleville, probably referring to the same event, attributed a decline in south-western Queensland to cyanide poisoning - see above.) There are also some comments on sources of mortality. Reports state that possums were killed in large numbers by foxes, cyanide, and eating prickly pear fruit. As for *P. cinereus*, there are also reports that they were protected from harvesting by the pear scrubs.

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[28] Queensland State Archives: Department of Agriculture and Stock. AGS/N350A file 08861. 1908. Memo from Stock Inspector McCarthy, 9/6/1908.

[29] Department of Agriculture and Stock. Annual Report 1908-1909. Native Animals Protection Act pp. 35-36.

[30] Department of Agriculture and Stock, Annual Report 1911-1912. Native Animals Protection Act pp. 27 - 28. *Queensland Parliamentary Papers* 1912.

[31] Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 2003. 1923. Letter from O.C. Norton, 1/5/1923.

[32] *The Courier-Mail*, 30/5/1936. Letter.

Possum numbers were very high in southern Queensland in the late 19th and early 20th centuries (Moreton, Darling Downs and South-western Districts, Figure 5). Numbers fell towards the 1920s and showed increases again through the 1920s. In the central and northern districts, numbers fell towards the 1920s and then increased through the rest of that decade, but more strongly than farther south (Figure 5). Numbers declined in the late 1920s or early 1930s in many Districts. Numbers in the Northern District were less volatile than in other Districts. The Districts in southern Queensland appear to fall into a similar pattern of irruption and decline as for koalas, but this is less evident in central and north Queensland. In the latter region, Districts with high numbers before the 1920s appear to have recovered

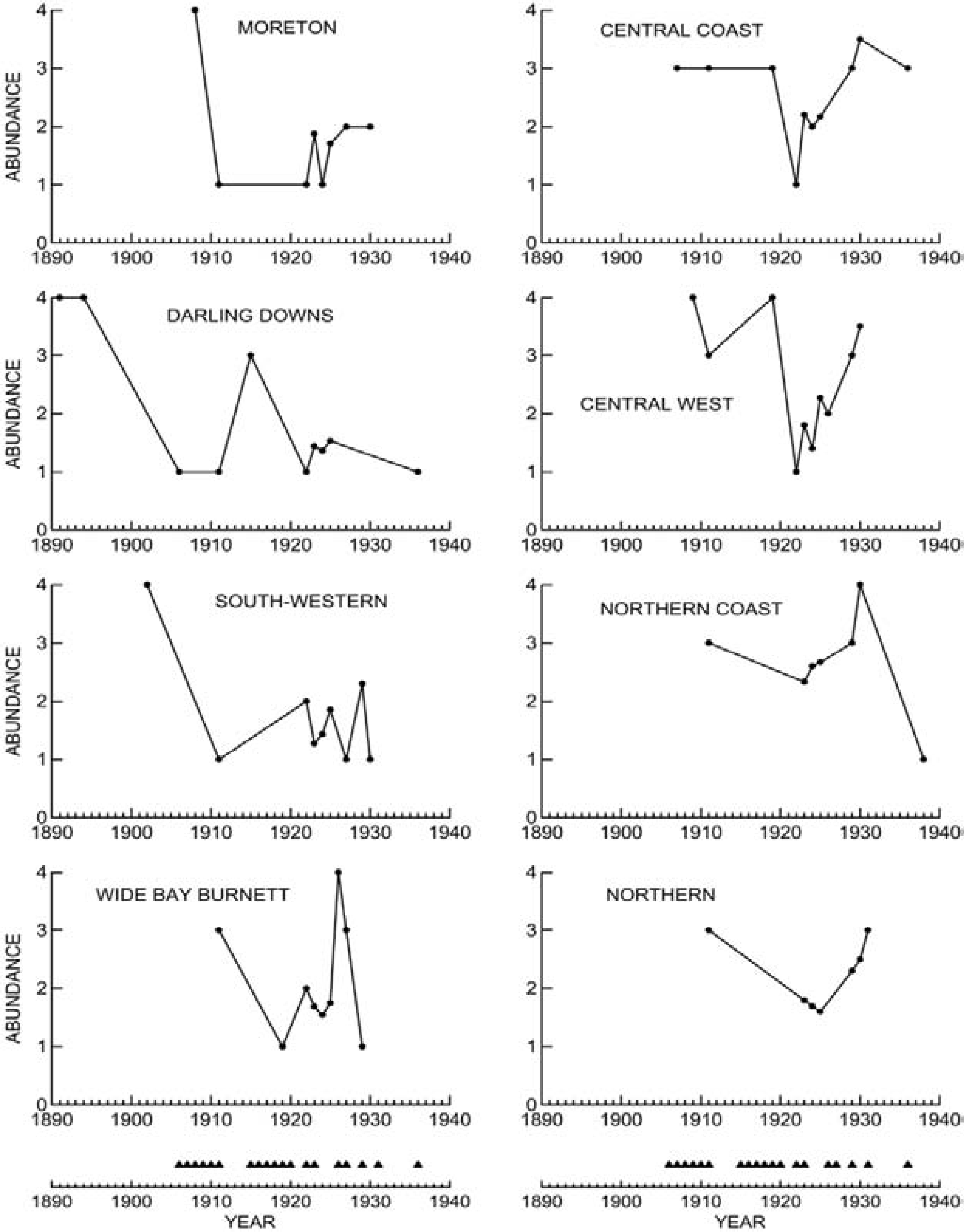

Figure 5. Records of possum numbers from 1890-1940. Symbols show mean status ranked in four categories, from scarce, 1, to abundant, 4. Solid triangles denote harvest years.

in numbers by the late 1920s. The timing of declines seems to have varied regionally. Within southern Queensland, possums were still common at Beaudesert in 1908 after they had declined at St George [28], (Kerle 2001).

Ranger W.E. Black's estimates of possum numbers in 1929 for each shire in the Northern, Northern Coast and Wide Bay and Burnett Opossum Districts showed that possums were common to abundant in about 80% of Northern Coast District, but scarce or absent in about 70% of Northern District and 90% of Wide Bay and Burnett District (Table 10).

Changes in populations do not correlate clearly with harvest periods (Figure 5). As for *P. cinereus*, heavy harvests in the early 1900s correlate broadly with declines in southern Queensland in the 1900s and 1910s, but not in central and northern Queensland. However, a strong fall in numbers around 1920 in many Districts correlates with an exceptionally high harvest in 1919 and 1920 totalling five million to six million possums (Hrdina and Gordon 2004). A severe drought occurred around the same time, but the harvest possibly provides the best explanation for this decline. Populations recovered later in the 1920s.

Severe droughts occurred in Queensland in 1895-1903, 1911-16, 1918-20, 1922-23, 1926-29 and 1933-38 (Bureau of Meteorology 1989, Figure 4). The strong fall in numbers of possums around 1920 correlates with major drought in 1918-20. However, fluctuation in population size does not otherwise correlate well with major drought.

Habitat loss

Several reports included comments on loss of habitat and its impact on *P. cinereus* or possums. Observers often stated that forest had been cleared closer in to settled areas, or on creek and river valleys, with intact forest left in rougher country and along watercourses. In 1923, Mr J. Hayes, Land Ranger at Toowoomba stated, "I consider the primary cause of their [i.e. native bears] decay is that the river, & creek flats, where grow the trees that Supply their favourite food, being usually good alluvial soil, is allways ringbarked for grass or cleared for cultivation; & the Bears were gradually driven to poorer & more unsuitable food, & large numbers starved out" [33]. The Officer in Charge of Police at Herberton in north Queensland in 1924 stated, "The scarcity of opossums and native bears is not attributable to disease, but to the placing of the district under close settlement" [18]. In a letter to the minister in 1936, Mr Hiron of Raglan observed that clearing of land for grazing destroyed the bear and possum as it did away with their natural food and shelter [25].

At the 1937 Fauna Authorities Conference [34], Ambrose Pratt claimed that bears in Queensland were afflicted with numerous diseases quite new to science due to malnutrition, as the bears were forced into land where their proper food trees were few and far between.

Discussion

P. cinereus health and disease

Diseases reported by observers that include prominent external symptoms are similar to those that occur now in wild *P. cinereus*, including chlamydial kerato-conjunctivitis and cystitis. Although only two definite tick infestations were reported from the harvest period, some accounts of "paralysis" might be due to tick paralysis. Elsewhere, there are relatively few accounts of severe tick infestation in wild *P. cinereus*. Martin and Handasyde (1999) report some localised severe tick problems. McMichen (1934) observed little tick *Ixodes holocyclus* infestation in a captive colony at Koala Park in Sydney. Gordon *et al.* (1988) found higher tick *Amblyomma triguttatum* loads in some animals affected by drought conditions in western Queensland. No reports were found of reproductive tract pathology or female infertility, and observers were probably unaware of it.

The prevalence of disease apparently was much higher in many areas than it is now as disease was commonly reported throughout the harvest period, and diseases were sufficiently common to be conspicuous to non-expert observers. Diseases were distributed throughout the State, but prevalence may have been relatively lower in north Queensland. As reports were more common then, disease was probably much more common in central Queensland, and possibly also on the Darling Downs, than was found by Gordon *et al.* (1990) in the 1970s and 1980s. The high number of reports from central Queensland correlates with high *P. cinereus* abundance then, as most reports came from the 1920s when central Queensland populations were at high levels.

Factors correlating with high levels of chlamydial disease include high population density and occurrence in the semi-arid zone. Most reports came from the Central West District in the inland semi-arid zone (Table 6) in the 1920s when populations were relatively high (Figure 3). Occurrence in a more extreme climate, particularly during long dry periods, might place *P. cinereus* in situations where they are more susceptible to infectious disease if animals were weakened due to their occurrence in marginal habitat with its poorer nutrition. Given the unsystematic nature of the data used here, this observation is indicative only.

Chlamydial disease has also been linked to loss of habitat (Ellis *et al.* 1993; Weigler *et al.* 1988), with a suggestion that deforestation leads to crowding and chronic stress, depressing defence and immune mechanisms, and resulting in the development of clinical disease (Weigler *et al.* 1988). However, the critical factor is likely to be high population density relative to the carrying capacity of the site, rather than stress, whether it results from loss of habitat or great expansion in population size. Higher density could either lead directly to higher rates of infection via contagion, or it could lead to poorer nutrition

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[33] Queensland State Archives: Department of Agriculture and Stock. AGS/J201 file 23/2003. 1923. Memo from Land Ranger Hayes, 13/2/1923.

[34] Queensland State Archives: Department of Agriculture and Stock. AGS/J1195 file 18382. 1937. Minutes of 1937 Fauna Authorities Conference 14-16 September 1937.

Table 10. Estimated status of possums in April 1929, Northern, Northern Coast and Wide Bay and Burnett Opossum Districts, showing area of District in each status category. Data from Ranger W.E. Black, Department of Agriculture and Stock. "No. shires" shows number of shires in each category per District. Source: Queensland State Archives: Department of Agriculture and Stock. AGS/J565 file 604. Memo from Ranger Black, 12/4/1929.

		Area (s. km) and Number of shires			
District		**Plentiful**	**Fairly Plentiful**	**Scarce**	**None**
Northern	Area	0	118,050	220,986	20,095
	No. shires		1	15	1
Northern Coast	Area	311	51,112	12,626	0
	No. shires		5	3	
Wide Bay Burnett	Area	0	5,128	67,055	2,331
	No. shires			17	1

(through increased competition for the available food), which in turn might increase susceptibility to disease. *P. cinereus* in captivity tolerates a great degree of crowding without any obvious increase in susceptibility to disease due to "stress" from crowding. Chlamydial disease rates in zoo colonies in south-eastern Queensland were found to vary between zoos and were not related to the size or density of the colony (Gordon 1996). The level of disease in zoos apparently depends on husbandry standards at each zoo, and chlamydial disease outbreaks at zoos have been attributed to a fall in nutritional standards and to the introduction of wild *P. cinereus* to the colony that transmitted disease to resident animals (Gordon 1996). Zoo colonies do not usually experience high levels of chlamydial disease if adequate standards of nutrition and hygiene are maintained.

In other States, there are accounts of disease associated with population irruptions. Martin and Handasyde (1999) give detailed accounts of chlamydial disease in irrupting populations in Victoria. At Bega in New South Wales, prior to a sharp drop in numbers from 1909-1910, koalas were said to be "very sick and dejected" and were popularly believed to be stricken with a disease, which resulted in "paralysis and eventual starvation" (Lunney and Leary 1988).

Demographic factors in *P. cinereus* populations

Information from observers and other sources deals with five main population phenomena – high rates of disease, fluctuation in population size, mass mortality, harvest mortality and loss of habitat. The impact of different factors on population dynamics is difficult to unravel as there were a number of possible major influences on population size and these factors may have interacted with each other.

Disease. The population impact of the disease is uncertain, although from knowledge of disease today we may speculate that it caused serious ongoing mortality, particularly when cystitis was present, and depressed population size. There is evidence of disease causing local scarcity on the Darling Downs in the 1980s (Gordon *et al.* 1990). Endemic disease, with its effect on female fertility, can reduce population growth over lengthy periods and hold population density at low levels (Gordon *et al.* 1990; Martin and Handasyde 1999; Penn *et al.* 2000).

Fluctuation in population size. Populations at a State-wide level were much higher during the harvest period than now (although some regions had very low numbers). The recurring episodes of mass mortality during hot weather indicated that *P. cinereus* populations were at abnormally high and unsustainable levels, supporting the proposal that population irruptions had occurred. There is little indication from reports of the cause of the high abundance.

Favourable weather has been linked to population expansion. The population crash described by Gordon *et al.* (1988) was preceded by six years of high rainfall when *P. cinereus* numbers presumably increased. It is likely that increased food availability, stimulated by rainfall, supported this increase. Although favourable weather may explain some local population expansion, over a broader scale and time frame this explanation fails. Populations in central Queensland were consistently high during the mid to late 1920s, although drought years were common during this period.

Mass mortality. Large scale mortality was common, although it is difficult to determine if such mortality occurred consistently throughout this period. This mortality appeared to be more common in inland areas in central and southern Queensland. Reported mortality was low in north Queensland.

Observers attributed mortality to various diseases. However, there is no certainty that the reported mortality was a result of the reported disease. The correlation with hot dry summers is mostly consistent with the report by Gordon *et al.* (1988) of a population crash at Mungalalla Creek. That event, however, differed in occurring in extremely hot weather with temperatures greater than 40 degrees C and defoliation of food trees. Much of the reported historical mortality probably occurred when abundant populations in sub-optimal habitat encountered drought during a dry summer. Recent studies show that *P. cinereus* can utilise a very wide range of communities in Queensland, but that density varies markedly (Melzer and Lamb 1994; Munks *et al.* 1996). Historical accounts of very high *P. cinereus* density imply that habitat utilisation must have been very broad, because high density would force *P. cinereus* to extend into sub-optimal habitat in larger numbers. This would make them more vulnerable to mass deaths when there was a hot dry summer. Alternatively, some of the mortality may have been a result of high prevalence of disease in abundant populations, leading to high mortality.

There is no reliable evidence of the population impact of the mass mortality. We may assume that it led to steep declines, but it is uncertain whether it was sufficiently high to cause scarcity or merely acted to prune populations back to a "carrying capacity" level. There were many reports of local scarcity. However, this scarcity, alternatively, may have resulted from the harvest or from infertility. The crash in hot weather reported by Gordon *et al.* (1988) did not lead to local scarcity. A population with normal reproductive rates should have a reasonable chance of recovering relatively quickly from intermittent large scale mortality, such as would result from a dry summer, depending on local factors affecting the population. It is likely that at least some (or many) local populations recovered from these episodes of mortality and were harvested again, since the harvest continued for a number of years and observers' reports implied recovery of local populations.

Harvest mortality. The population impact of the harvest mortality is likely to have been complex and dependent on local factors. In some Opossum Districts population declines correlated with harvesting, whereas in others, populations expanded following harvest and declines occurred later. The latter declines could not be attributed to harvesting. The decline in some Districts in the early 1920s following the very high harvest of 1919-1920 may mean that the harvest rate was far too high for sustainability, whereas harvesting at lower rates may have been sustainable in the short term. It is also possible that harvests led to severe local declines and local scarcity. Many reports at the time stated that this happened.

It is often said that the harvest led to the State-wide decline of *P. cinereus*. The evidence presented in this paper does not provide much support for this idea, and partly contradicts it. For example, abundant populations occurred in Central Coast, Central West and Northern Coast Districts well after the last harvest. A substantial *P. cinereus* decline apparently occurred at some time. This probably occurred in the 1900s-1910s for southern Queensland and late 1920s-1930s for central Queensland. The State population was high enough to sustain the harvest up until 1927 at least. A seriously declining population might not be expected to sustain such a harvest. Although there is no certainty about the impact of the harvest on *P. cinereus* populations, the most probable outcome is that the harvest did not cause a significant State-wide decline, although there probably were severe regional declines due to high local harvests.

Harvests interacted with other population factors including natural mortality and, probably, infertility in some populations. Harvests and visible mass mortality possibly substituted to some extent. Observers commonly stated that harvests were necessary to keep populations "healthy", i.e. to keep populations at a level where mass mortality could be avoided and prevalence of disease was low. When mass mortality occurred, it was common for trappers to lobby governments for an open season to "save" the skins that would otherwise be lost due to natural deaths.

If significant infertility were present, then high rates of harvest mortality acting on populations with high rates of infertility should have had a very serious impact on numbers. There is no information on prevalence of infertility at that time. In recent studies, it has been found commonly in populations with high abundance, and, given the high abundance in many areas, it is possible that infertility was substantial.

Loss of habitat. The decline from peak population levels has included an overall reduction in the State population size and increased scarcity within intact habitat. Clearing of habitat can readily account for the former, but not for the latter. Observers provided little information on the impact of habitat loss on populations. It undoubtedly caused local contraction in distribution and overall decline in population size. Loss of more favourable habitats such as communities on creek lines and alluvial flats, which were cleared more extensively, may have also led to overall lower average densities (i.e. animals / ha) in the remaining less favourable habitat.

Significant loss of habitat has occurred since European settlement (Wells *et al.* 1984, cited in Pahl *et al.* 1990; Melzer *et al.* 2000). It is likely that most of the early clearing was concentrated on fertile stream valleys. This kind of clearing would have had a severe impact on *P. cinereus* and *T. vulpecula*, resulting in local declines in numbers. However, substantial areas of forest and woodland would have remained in other land types, at least some of which would have formed habitat for *P. cinereus* and possums, although probably of poorer quality, so that broad scale distribution should not have been seriously affected. A detailed analysis of koala habitat loss in Noosa Shire, south-eastern Queensland showed that greatest loss occurred from 1890-1910 (linked to dairying) and from 1970-1999 (linked to forestry plantations) (Seabrook *et al.* 2003). The total area of koala habitat, including primary and secondary habitat, has now halved and habitat fragmentation has increased greatly. Proportion of habitat loss consisted of 30 percent primary habitat, 65 percent habitat class 2A, 33 percent habitat class 2B and 69 percent habitat class 2C.

P. cinereus population expansion

Explanations for the expansion phase of the *P. cinereus* irruption generally postulate release from controlling factors following European settlement and include:

- Decline in Aboriginal hunting (Parris 1948; Warneke 1978; Strahan and Martin 1982; Martin and Handasyde 1999).
- Decline in dingo predation (Strahan and Martin 1982).
- Expansion into re-growth vegetation following settlement and land development (Melzer *et* al. 2000; this paper).
- Increase in availability of nitrogenous food (Degabriele 1981).
- A wave of eucalypt dieback following early land development, with increased availability of nitrogen-rich foliage in the early stages of dieback (Jurskis and Turner 2002; Jurskis 2002).

- Release from plant defences: phyto-oestrogens (Obendorf 1981; Strahan and Martin 1982); and defensive leaf compounds - formylated phloroglucinol compounds (FPCs, Moore and Foley 2000).

Aboriginal hunting. Aboriginal population size decreased significantly following European settlement and two factors were of major importance, mortality from introduced disease and decline in birth rates (this and the following information is from Horton 1994, and Campbell 2002). Major diseases included smallpox, typhoid, tuberculosis, diphtheria, whooping cough, influenza, pneumonia and measles. Major outbreaks of smallpox, possibly introduced from the north by Indonesian visitors, occurred in New South Wales, Queensland, Victoria and South Australia from 1789-91, and across eastern Australia from Queensland to South Australia from 1828-32. A third outbreak occurred in the late 1860s. Mortality rates are unknown, but there is evidence that 20-75% of those infected died. Smallpox in many regions preceded European settlement and the debilitating effect of disease could prevent normal food-gathering and lead to death from starvation or secondary infections.

Irruptions of translocated *P. cinereus* populations on islands and in mainland habitat islands often took less than 20 years after translocation to reach a peak (Martin and Handasyde 1999). For *P. cinereus*, release from Aboriginal hunting was probably most significant at the time of the great human mortality that resulted from introduced disease, around 1830 and earlier, not a few decades later when Aboriginal tribal life and traditional hunting practices finally broke down. If Aboriginal hunting declined severely by about 1830, *P. cinereus* irruptions should have been evident by the late 1840s. If this interpretation is correct, then decrease in Aboriginal predation does not correlate with the timing of the central Queensland population expansion (probably from 1910-1920), and probably also the southern Queensland expansion (probably in late 19th century) and others farther south. Southern mainland populations are thought to have commenced expansion in the late 1850s, possibly peaking in the 1860s and 1870s. In addition, north Queensland koala populations show little evidence that any broad scale expansion occurred at all, despite the destruction of Aboriginal communities there.

Dingo predation. Release from dingo predation might provide a more plausible explanation of *P. cinereus* expansions as dingo declines presumably occurred later. Information on the timing and extent of dingo declines is less accurate. However, any dingo declines were probably linked to control operations and were more patchy and not uniform across broad regions. Glen and Short (2000) suggest that control efforts by both pastoralists and hunters may have led to the decline of the dingo in New South Wales where it has disappeared over much of its former range. Dingo declines are therefore unlikely to provide an adequate correlation with the broad scale *P. cinereus* population expansion. Jarman and Johnson (1977) found that the reduction of dingo populations did not correlate with irruptions of kangaroos, wallabies, "padamelons", rat kangaroos, hares or rabbits.

Re-growth vegetation. Jarman and Johnson (1977) found evidence that macropod population irruptions in the late 19th century correlated with the development of land following European settlement, and presumably resulted from an expansion of macropod food supply. A similar mechanism could account for the *P. cinereus* expansion. One possibility may be that koala population expansion was supported by the development of abundant regrowth vegetation and/or increase in plant density after European settlement. Following early land development, there was development of regrowth vegetation after initial attempts at clearing, and increase in tree density due to suppression of fire or other changes to fire regime in many other plant communities. Either of these phenomena might have provided *P. cinereus* with a substantial increase in food resources and may have stimulated population expansion. As settlement and development proceeded from south to north, this proposal also provides an explanation for the delay in expansion of *P. cinereus* populations in central Queensland. The absence of severe population fluctuation in north Queensland correlates with lower rates of tree clearing and lower intensity of agricultural development in that region in the early 20th century.

Nitrogenous food. Degabriele (1981) related *P. cinereus* numbers to availability of nitrogenous food, and suggested that local "outbreaks" of *P. cinereus* populations occurred when population growth was boosted by a flush of new growth rich in nitrogen when favourable weather resulted in more, or more prolonged, growth of fresh foliage. He also suggested that coppicing had a similar effect in maintaining nitrogen rich food by stimulating a flush of new growth. Young trees might also provide such a growth flush and support higher densities. Moore and Foley (2000), however, discuss problems with this idea.

Eucalypt dieback. A wave of eucalypt dieback occurred in the late 19th century (Jurskis 2002). Dieback has been associated with changes in land management, including reduced occurrence of low intensity fire and nutrient enrichment (Jurskis 2002; Jurskis and Turner 2002; Jurskis *et al.* 2003). Landsberg (1990) found that dieback foliage of *Eucalyptus blakelyi* is nutritionally superior for insect herbivores, with more nitrogen, and that it was subject to higher levels of insect herbivory and defoliation. Jurskis (2002) suggested that folivores, including koalas, respond to the nutritious foliage that is produced in dieback trees, leading to expansion of folivore populations and accelerated defoliation of eucalypts. High levels of herbivory are more likely on stressed plants, because agents causing dieback may cause improvements in the nutrition and palatability of eucalypt leaves (Jurskis and Turner 2002).

Plant defences. A more speculative proposal is based on the development of plant defences in response to browsing pressure. *P. cinereus* populations expanding into regrowth vegetation might encounter food plants with poorly developed defences against browsing. This proposal requires that, in response to browsing pressure, either (a) plant chemical defences increase, or (b) plant species composition changes to favour herbivore resistant species (which is unlikely in the case of *P. cinereus*). Jarman and Johnson (1977) suggested that changes in plant defences might have influenced the numbers of irruptive grazing mammals. Strahan and Martin (1982) suggested that reproductive tract disease and infertility might result from phyto-oestrogens in eucalypt foliage, based on observed effects of phyto-oestrogens in sheep (Shutt 1976). Recent work (Lawler *et al.* 1998; Moore and Foley 2000) has shown that chemical defences are present in eucalypts, and they succeeded in identifying eucalypt leaf compounds, formylated phloroglucinol compounds, which inhibit mammalian herbivory and may finally solve the mystery of *P. cinereus* diet selection.

P. cinereus population decline

It is difficult now to identify the role played by various population factors in causing the koala population declines.

Harvest mortality. The evidence from this paper provides little support for the proposal that harvest mortality was an overall cause of the declines as there are some Opossum Districts where population numbers stayed high or increased following the harvest. Subsequent declines were due to other causes of mass mortality. If *P. cinereus* was undergoing a herbivore irruption (see below), the harvest may be seen as fortuitous or opportunistic in taking advantage of the underlying demographic process. See Caughley (1976, p 241, 1977, p 131) for a description of the impact of added mortality on the progress of an irruption pattern. For a system trending towards equilibrium, modelling shows that addition of a predator may displace the equilibrium herbivore population to a lower level and may dampen the oscillations. Harvesting a koala population undergoing an irruptive fluctuation might act to limit the upper peaks of the oscillations, accelerate the decline and eventually result in an equilibrium population at a lower level.

Loss of habitat. Clearing of forest and woodland undoubtedly is a major cause of the contraction in size of the overall State population, and a probably massive contraction in local distribution, but it does not explain the great declines in density in the remaining good habitat. The latter factor seems to form a major component of the population decline. At the time of the harvest, habitat loss consisted of selective clearing of particular land types and fragmentation of the vegetation cover over the landscape, rather than broad scale clearing. It has been suggested that loss of habitat may cause crowding, which in turn precipitates other mortality factors such as infectious disease, either due to increased density or to stress effects (Weigler *et al.* 1988). During the early 20th century, large areas of forest and woodland remained and it is debatable that habitat loss would lead to excessive crowding in such a landscape. Many animals would possibly react to habitat loss by dispersal into more marginal habitat, rather than by concentration in the remaining highly favourable habitat.

Natural mortality. Mortality during hot weather, probably of animals occurring in poorer habitat, does not in itself seem to account for the decline as it may have simply served to reduce populations to a carrying capacity level. However, it could have interacted with other sources of mortality during declines.

Dieback. Jurskis (2002) has linked koala decline to the final stages of eucalypt dieback. As food becomes depleted in dieback trees, koala populations must also decline. Poor nutrition in such populations could also provide an explanation of disease outbreaks in declining populations, which are commonly associated with declines.

Disease. Mortality from disease may provide a better explanation of long term declines. However, the quality of information on the occurrence of disease at the time is very poor and it is difficult to determine now exactly how disease was affecting populations. Disease is commonly associated with descriptions of decline. Mr F. Rolleston [21] described the decline of koala populations at Mackay as follows: "These open seasons had nothing to do with the decline of koalas, as there were hundreds to be seen after 1927 [the last koala open season]. In 1928 I counted 10 in one tree. Somewhere about the mid-1930s a strange illness struck the koalas and they could be found at the foot of trees, with eyes gummed and too weak to climb. After World War II there were still big forests of blue gums where once koalas were plentiful, but they had long disappeared." (Blue gum *E. tereticornis* communities on watercourses and alluvial areas often provide very favourable koala habitat in Queensland.) Le Souef and Burrell (1926) attributed *P. cinereus* scarcity "over the greater part of its range" to disease that killed "millions" in 1887-1889 and 1900-1903.

However, a one-off disease event in itself does not seem to provide a mechanism for more or less permanent, or at least long term, suppression of population size. A more appealing explanation of the decline comes from interaction between the *P. cinereus* population and its eucalypt habitat.

Herbivore irruption and long term population fluctuation in *P. cinereus*

P. cinereus populations are generally believed to have undergone a very large expansion from about mid 19th century, followed by a serious decline in the late 19th to early 20th century, probably declining to levels lower than the starting point. In central Victoria for example, koalas were unrecorded prior to 1850, a few were seen in the early 1850s, and populations peaked between 1870 and 1890 (Parris 1948). At Bega in New South Wales, populations irrupted during the 1860s, were at high levels from approximately 1870 to 1905, declined sharply from 1905-1909 (Lunney and Leary 1988), and have remained rare. The population changes in Queensland in the early 20th century appear to be part of this broad scale fluctuation. Although no evidence was found of a low phase preceding the peak periods in Queensland, this is probably due to the absence of reports from the relevant periods, rather than to absence of this phase.

Although it is sometimes said, particularly with regard to island populations, that Queensland (and New South Wales) populations differ from those of Victoria in that they do not exhibit local irruptions and excessively high abundance, the Queensland population fluctuations appear similar to those occurring in Victorian populations. Queensland populations achieved high growth rates that resulted in unsustainable population densities and, eventually, mass mortality, which is essentially similar to the phenomena reported from Victoria. They possibly differed from Victorian populations in perhaps failing to reach extremely high abundance (up to nine koalas per ha in Victoria, Martin and Handasyde 1999) or to cause excessive defoliation of trees through over-browsing - no reports were found of over-browsing or tree defoliation during the harvest period in Queensland. Wildlife managers should therefore be cautious in assuming that the southern problems of over-population cannot occur in Queensland.

There is evidence of latitudinal difference in the timing and extent of population fluctuations in Queensland. Farther south, in New South Wales and Victoria, the expansion and decline may have occurred slightly earlier, and it is likely that there was a south to north wave of population expansion and contraction. This pattern correlates broadly with the timing and intensity of development of land for pasture and agriculture in eastern Australia.

The *P. cinereus* population fluctuations described here are consistent with Caughley's (1976, 1977) model of herbivore irruptions. The *P. cinereus* irruptions are also similar to irruptions that occurred in other mammals following European settlement, attributed to expansion of food supply (Jarman and Johnson 1977), and may have similar causes. "Whenever an ungulate population is faced with a standing crop of vegetation in excess of that needed for maintenance and replacement of the animals, an eruption and crash is the inevitable consequence" (Caughley 1976). An irruption is defined as an increase in numbers over at least two generations followed by a marked decline (Caughley 1970). In Caughley's model, the herbivore population and the vegetation usually proceed through a series of dampened oscillations until equilibrium is reached. The pattern of irruption and decline arises from interaction between animals and their food supply. The expansion in population size is a response to an increase in food supply, and the decline is thought to be due to depletion of food resources by over grazing. Caughley (1970) gives examples of ungulate irruptions and declines.

Depletion of *P. cinereus* food supply in Queensland by over-browsing has not been demonstrated, but there are speculative explanations that might account for a decline. In southern States at least, very high density populations may over-browse their food. If expansion resulted from dieback, food availability will decline greatly due to over-browsing in late stage dieback, leading to a severe decline in *P. cinereus* populations. If population expansion was triggered by the availability of regrowth vegetation, as trees matured towards climax communities the quality of food might lessen, providing *P. cinereus* with a food resource of diminishing quality that is susceptible to over-browsing and that leads to population decline. Mobilisation of plant defences in response to browsing might also reduce food availability. Alternatively, infectious disease in dense populations, leading to female infertility, might also cause population decline (Gordon *et al.* 1990; Martin and Handasyde 1999; Penn *et al.* 2000) and accentuate the impact of a reduction in availability of food. Continuing female infertility could lead to a lag in recovery and long-term suppression of population size.

Conclusions - *P. cinereus* population fluctuations

A number of hypotheses have been put forward to explain the expansion phase of the historical *P. cinereus* population fluctuations. The cause of the decline and subsequent scarcity has received less detailed attention. At one level it may be seen as a correction of the preceding excessive abundance. However, there is still a need to identify the actual processes involved. A key problem is the impression that in at least some (or many) areas the population size appears to have dropped well below the levels (carrying capacity) that would be set by the habitat, to a point of scarcity or even local extinction, with populations then remaining depressed for lengthy periods before recovering. Populations in the Darlings Downs Opossum District dropped to very low levels after 1900 and apparently stayed low into possibly the late 1940s or early 1950s (Figure 3). In the Moreton District there were low populations from the late 1900s to the mid-1920s (Figure 3). In the Central West, populations also entered a period of long-term scarcity with delayed recovery (Rolfe 2001). In the early 20th century, and also in recent times, it is possible to identify sites where koala numbers can be plausibly related to a presumed carrying capacity, but conversely, sites can also be found where scarcity seems to be independent of overt habitat factors and other factors are limiting population size.

The population declines in the early 20th century possibly undershot the carrying capacity greatly in at least some Opossum Districts, resulting in population levels well below the carrying capacity, and local scarcity. Populations then showed delayed recovery, with koalas remaining scarce for about three to four decades in at least some Districts. Populations in Queensland that have recovered since then have probably not reached the levels of abundance (expressed as density - number of koalas per ha of forest or woodland) attained by peak populations during the harvest period. It is not clear if they have recovered to the pre-European levels, but they may have done so.

We suggest that the most likely explanation for the historical population expansion in Queensland is that it was a response to either (or both) the development of regrowth vegetation or eucalypt dieback, both of which might lead to an increase in food supply. That is, *P. cinereus* experienced a qualitative improvement in habitat quality associated with land development. Differences in timing of land development from south to north can explain the latitudinal difference in timing of irruptions. Release from predator control (Aboriginal or dingo) does not fit well with the timing or location of the irruptions.

Identification of the factors causing the historical decline, to the point of scarcity, is more difficult. Several factors regularly acted to prune populations to a lower level, either in combination or separately in different locations ("climatic" mortality in hot dry summers, disease mortality, harvest mortality), but often did not seem to succeed in preventing population recovery again. These factors do not seem to provide an adequate explanation of the decline to very low levels, and subsequent long-term scarcity in many areas. Even in areas where this mortality was so severe as to push populations to very low levels, there should have been recovery once the mortality ceased. Harvest mortality was regulated legally and should not have been important after 1927 (when the harvest ceased), and the other two major mortality sources were almost certainly density dependent, and so should not have been very important during periods of low numbers. Periods of severe climate may have delayed recovery in some areas, but again, populations should have recovered once climatic conditions improved. At Mungalalla Creek in 1980 (Gordon 1988), *P. cinereus* populations expanded following several years of high rainfall, encountered a drought and hot summer and crashed to a lower level, and probably stabilized at that level. They did not become scarce but remained in good numbers in favourable habitat. There were no obvious habitat changes (such as clearing or vegetation regrowth) or disease outbreaks that might explain the events. Peak populations had expanded into poorer quality habitat whereas the final populations contracted back into the most favourable habitats. The process appeared to result entirely from climatic changes causing mortality of koalas in the poorer habitats. Events similar to this must have occurred during the harvest period, probably frequently, but they do not seem to be able to explain severe decline and long-term scarcity.

A decrease in food availability (possibly habitat change due to maturation of regrowth vegetation or degradation of eucalypt communities subject to dieback), leading to qualitative habitat change, probably provides the best explanation of the decline. If this was accompanied by severe outbreaks of chlamydial disease (due to poor nutrition), it might explain the severity of the decline to a point well below carrying capacity. This hypothesis is also consistent with observations of *P. cinereus* failing to utilise habitats that superficially appear suitable for it. These factors probably interacted with declines resulting from intensive land development and severe loss of favourable habitat in some areas, including parts of Moreton, Wide Bay and Burnett and Darling Downs Opossum Districts.

We suggest that one or more of the following could explain the long-term depression of population size in areas that still have large areas of apparently favourable habitat:

- Female infertility and depressed reproductive rates resulting from chlamydial infection, possibly supplemented by ongoing mortality caused by the disease, could probably act to delay population recovery. A process similar to this has been observed in a population studied at Oakey (Gordon *et al.* 1990).
- In areas where populations were severely reduced, delay in population recovery could also be explained partly by the difficulty of recovery from a low base. If populations were reduced to small nucleus populations, it might take many years for recovery, particularly if climatic conditions were unfavourable.
- A severe downturn in habitat quality (due to factors listed above) could lead to long-term scarcity. Population recovery might only occur when vegetation regrowth or vegetation expansion occurred in the area.

Some of the present scarcity must also be due to severe clearing. Clearing of the most favourable habitat would undoubtedly lead to permanent scarcity where the only habitat remaining was of poorer quality, such as has been suggested for the Bega Valley in southern New South Wales (Lunney and Leary 1988). However, this did not occur everywhere. In Noosa Shire, areas identified as primary habitat were least affected by clearing, with 70% of primary habitat remaining (Seabrook *et al.* 2003). Similarly, in parts of the State where agricultural and pastoral development has been less intensive, large areas of *P. cinereus* habitat remained into the late 20th century at least, or are still present (e.g. much of Central Coast, Central West, South-Western, Northern Coast and Northern Districts, and parts of other Districts).

Finally, during peak populations it is likely that *P. cinereus* occupied poorer habitats at higher densities than were sustainable over a long term, due to dispersal of animals from more optimal habitats. Such habitats might now support only low-density populations, giving an appearance of undue contraction in size.

Possum populations

From the reports and anecdotal accounts of high abundance we may infer that population irruptions of possums occurred in southern Queensland around 1900 and earlier, followed by declines, with a secondary increase again in the 1920s, following a similar pattern to herbivore irruptions (Caughley 1977). In central Queensland, populations were high in the 1910s and 1920s, apart from a steep dip around 1922. This pattern shows that there was a latitudinal difference in population dynamics between southern and central Queensland, as happened for koalas also. As for *P. cinereus*, the decline phase of the irruption occurred later in central than in southern Queensland. There is less certainty about population trends in north Queensland, but population levels in Figure 5 imply that high abundance was attained and populations probably were irruptive, unlike koala populations in the north. Changes in numbers of possums do not correlate as closely with major aspects of the development of land for pastoralism and agriculture as do the changes in *P. cinereus* numbers. However, it is likely that development provides part of the explanation for possum abundance patterns. It is hard to identify the specific factors responsible for the expansion and decline, beyond a general observation that *T. vulpecula* populations may have been affected by changes in ground herbage (Jarman and Johnson 1977). The reliance of *T. vulpecula* on ground feeding may make its numbers susceptible to changes in the composition and quantity of ground herbage resulting from changes in land management or changes in fire regime. Such factors could vary greatly at a local level and would have largely gone unrecorded historically. If a change in ground herbage and pastures was sufficient to trigger an irruption, then *T. vulpecula* would be more susceptible to this phenomenon than *P. cinereus*, which possibly requires changes in the tree stratum.

The cause of the declines is uncertain. In some reports, the decline is blamed on the use of cyanide baits and the arrival of foxes in Queensland. However, according to herbivore irruption models the decline could be due to depletion of food supply. The latter explanation seems feasible for a ground feeding possum like *T. vulpecula* which could be subject to competition from other ground dwelling herbivores.

T. vulpecula in Tasmania, which is free of fox predation, reaches densities of eight per ha in partly developed country (Tasmanian Parks and Wildlife Service 1999). The anecdote of *T. vulpecula* in lucerne crops at Ballandean (see above), implies that density was much higher than that attained by peak populations in Queensland now. As for *P. cinereus*, no evidence was found of a low phase preceding the peak periods. This probably is due to the absence of reports from the relevant periods, rather than to absence of a low phase.

It is uncertain which species of possums underwent population irruptions. *T. vulpecula* was certainly the main species, but others may have also been irruptive, including *P. peregrinus*, as there were high harvests of ringtails (Hrdina and Gordon 2004) as well as brushtails. As was suggested for *P. cinereus*, we may speculate that *P. peregrinus* populations were influenced by regrowth of vegetation following clearing, but we did not discover any empirical evidence in support of this explanation.

The possum irruption is similar to those of southern States. Lunney and Leary (1988) showed that *T. vulpecula* at Bega were highly abundant from about 1860-1900 and underwent a decline from about the end of the first decade of the 20th century. Brushtail possums in New England, New South Wales, were scarce after 1834 when the area was first settled. However, by the 1870s they had increased greatly and had become pests in maize crops (Jarman and Johnson 1977). *T. vulpecula* also exhibited short-term and localised irruptions and crashes as reported by Kerle (2001) at St George from 1881-1896. Jarman and Johnson (1977) link the possum irruptions in New England to improved food supply resulting from changes in pasture composition and productivity, rather than from cropping, suggesting that the small area under crops then was insufficient to support the enormous increase in numbers. Land-use changes included ring-barking and the introduction of exotic pasture species.

The possum harvest appears to have been sustainable on a State-wide basis, at least in the short term until 1936 when harvesting ceased. Observers suggest that harvests sometimes, or often, had a severe local impact on possum populations, leading to local scarcity. The harvest in Tasmania has been shown to have an impact on possum numbers (Tasmanian Parks and Wildlife Service 1999).

Possum harvests occurred much more frequently than *P. cinereus* harvests and possum populations were subject to fairly regular hunting pressure (Hrdina and Gordon 2004). Closed seasons occurred in 1912-14, 1921, 1924-25, 1928, 1930, 1932-35. The duration of open seasons when pelts could be legally obtained and sold under the Acts amounted in total to 6 years and 18 days, with 19 open seasons in 31 years (from 1906-1936), averaging one season every 1.6 years (Hrdina and Gordon 2004).

Possum harvests ranged from about 400,000-3,000,000 per annum, and were commonly greater than 1,000,000 per annum (Hrdina and Gordon 2004). The average known take of possums was 1,829,580 animals per open season. The harvest was sustained at this level throughout the 30-year harvest period. Harvest size was much greater than the size of corresponding *P. cinereus* harvests (Hrdina and Gordon 2004), indicating the much greater abundance of possums. It is not known with certainty what affected the annual variation in size of the harvest each year, that is, supply or demand. However, there is evidence of strong fluctuation in market demand over the period (Hrdina and Gordon 2004).

Harvests in Tasmania from 1923-36 averaged about 53,000 *T. vulpecula* per season during nine open seasons. The average take per season in Queensland during the same period was 1,812,832 possums during six open seasons (Hrdina and Gordon 2004). The species composition is unknown but is likely to have comprised mainly *T. vulpecula*, but with a substantial take of *P. peregrinus* also (up to about 20 percent, Hrdina and Gordon 2004) and possibly *T. caninus*. In the late 1970s, the Tasmanian harvest sometimes reached nearly 300,000 *T. vulpecula* per annum and harvests of over 100,000 have been common. Numbers taken in Tasmania have fallen substantially since about 1980 due to a fall in demand (Tasmanian Parks and Wildlife Service 1999).

At present, *T. vulpecula* and *P. peregrinus* are relatively common in many parts of Queensland, but are thought to occur in much lower densities than they did during the early 20th century. Loss of habitat can account for at least part of the overall decline in population size in the State, but not for the decline in local density in intact habitat. It is not clear how current densities relate to pre-European densities. Regional fauna surveys carried out in the last few decades have usually found these species to be uncommon to common in status, but not abundant (e.g. Kirkpatrick 1966; Lavery and Johnson 1968; McEvoy and Kirkpatrick 1971; Lavery and Johnson 1974; McEvoy and McDonald 1979; Crossman and Reimer 1986; McFarland *et al.* 1999).

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APPENDIX I

Appendix 1. Annual mean status of koalas and possums in each Opossum District. 'n' shows number of reports of status for each category, mean = mean status, sd = standard deviation. Districts: CC = Central Coast, CW = Central West, DD = Darling Downs, M = Moreton, N = Northern, NC = Northern Coast, SW= South-western, WB = Wide Bay and Burnett. See "Methods" section for explanation of the calculation of mean status.

Year	Opossum district																							
	CC			CW			DD			M			N			NC			SW			WB		
	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd
Koala																								
1890							1	4																
1896							1	4																
1897							2	4	0															
1900							1	1		1	4													
1902										1	1													
1903																			1	4				
1907	1	1								2	3.5	0.7												
1908										2	1	0												
1910																			1	4				
1915							1	1														1	3	
1919				1	4								1	2								2	2.5	2.1
1920																			1	1		1	4	
1921										1	1													
1922	1	1		1	1		2	1	0	2	1	0							2	1	0	2	2	1.4
1923	31	2.1	1	26	2.2	1	25	1.1	0.4	8	1.4	0.5	64	1.2	0.4	24	2	0.9	33	1.2	0.4	16	1.3	0.6
1924	19	2.2	1.2	14	2.6	1.2	20	1.1	0.2	6	1	0	53	1.1	0.3	13	1.6	1	26	1.2	0.5	14	1.1	0.4
1925	9	2.9	0.6	12	2.8	1	17	1.1	0.2	11	1	0	6	1	0	3	3	1	14	1.4	0.5	4	1.3	0.5
1926	3	3.3	1.2	6	2.8	1.2							1	1					1	1		1	1	
1927	5	2.6	0.9	2	3.5	0.7	5	1	0	7	1.4	1.1				1	1		1	1		2	2	1.4
1928																1	4							
1929	1	3		1	3								3	1	0	2	3	0	3	1	0	1	1	
1930	2	3.5	0.7	2	3.5	0.7				1	2		2	1	0	2	4	0	1	1				
1931													1	1										
1932				1	3											1	4							
1934	1	4																						
1936	1	1					1	1																
1937	1	3																						
1938																1	1							
1942																1	3							
Possum																								
1869							1	4																
1888							1	4																
1891							1	4																
1894							1	4																
1902																			1	4				
1906							1	1																
1907	1	3																						
1909				1	4																			
1908										1	4													
1911	1	3		1	3		1	1		1	1		1	3		1	3		1	1		1	3	

APPENDIX I

Year	Opossum district																							
	CC			CW			DD			M			N			NC			SW			WB		
	n	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**
1915							1	3																
1919	1	3		1	4																	1	1	
1922	1	1		1	1		3	1	0	2	1	0							2	2	1.4	2	2	1.4
1923	30	2.2	1	25	1.8	0.8	25	1.4	0.6	8	1.9	0.6	64	1.8	0.9	21	2.3	1	33	1.3	0.6	16	1.7	0.7
1924	12	2	1	10	1.4	0.7	11	1.4	0.7	4	1	0	36	1.7	1	10	2.6	1	23	1.4	0.7	11	1.5	0.9
1925	6	2.2	0.8	11	2.3	0.8	15	1.5	0.5	10	1.7	0.7	5	1.6	0.5	3	2.7	0.6	14	1.9	0.9	4	1.8	0.5
1926				1	2																	1	4	
1927										3	2	1.7							1	1		1	3	
1929	1	3		1	3								3	2.3	1.2	2	3	0	3	2.7	1.5	1	1	
1930	2	3.5	0.7	2	3.5	0.7				1	2		2	2.5	2.1	1	4		1	1				
1931													3	3	1.7									
1936	2	3	1.4				2	1	0															
1938																1	1							